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Estimated Preseason Abundance in the California Dungeness Crab (*Cancer magister*) Fisheries

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METHOT, R. D. JR., AND L. W. BOTSFORD. 1982. Estimated preseason abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39: 1077–1083.

Annual preseason abundance for the central and northern California Dungeness crab (*Cancer magister*) fisheries is estimated from the decline in catch per unit of effort (CPUE) within each fishing season. The results support the common assumption that a large fraction of the available, legal size, male crabs are harvested each year; however, we noted regular changes in this fraction and also that it is rarely as high as previously assumed. In central California, annual exploitation rate was 92% during 1951–56 and declined to 72% following the collapse of the fishery. In northern California the annual exploitation rate varies with the 10-yr cycle of catch: 69% during the last few high catch years of each cycle, 84% in the first low catch year, and 54% during remaining low catch years and the first high catch year. The second high catch years are exceptions to a high exploitation rate. CPUE was saturated (i.e. did not decline) throughout the 1957 and 1977 fishing seasons. The large size of male crabs in the third and fourth high catch years also indicates high escapement in the second high catch years. Individual year-classes apparently may dominate the fishery for several years. This indicates that the time series of population abundance and recruitment is not as smoothly cyclic as the catch record.

Key words: dungeness crab, *Cancer magister*; abundance, recruitment, catch per unit of effort

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Le déclin des prises par unité d'effort (PUE) dans le cours de chaque saison de pêche a servi à estimer l'abondance présaisonnière annuelle du crabe dormeur (*Cancer magister*) dans les pêcheries du centre et du nord de la Californie. Les résultats confirment l'hypothèse commune qu'une grande partie des crabes mâles de taille légale disponibles sont récoltés chaque année; cependant, nous observons des changements réguliers de cette fraction et qu'en outre, elle est rarement aussi élevée qu'on le croyait. Dans le centre de la Californie, le taux d'exploitation annuel était de 92 % en 1951−56 et il diminua à 72 % après l'affaissement de la pêcherie. Dans le nord, le taux d'exploitation annuel varie selon le cycle de 10 ans des prises : 69 % dans les quelques dernières années de fortes prises de chaque cycle, 84 % la première année de faibles prises et 54 % les autres années de faibles prises et la première année de fortes prises. Les deuxièmes années de fortes prises font exception à un taux d'exploitation élevé. Pendant toutes les saisons de pêche de 1957 à 1977, les PUE furent saturées (c.-à-d. ne diminuèrent pas). À en juger par la grande taille des crabes mâles dans les troisièmes et quatrièmes années de fortes prises, un grand nombre évitent la capture les deuxièmes années de fortes prises. Des classes d'âge individuelles peuvent, semble-t-il, dominer les prises de plusieurs années. Ceci indique que la série de l'abondance des populations et de leur recrutement ne montre pas de cycle aussi régulier que celui des prises.

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FLUCTUATIONS in the annual catch of Dungeness crab (*Cancer magister*) have been the subject of extensive research. In central California the mean annual catch has declined from 2.11 Mkg during 1951−61 to only 0.31 Mkg during 1962−77. In northern California the catch has cycled over a greater range with a period of 9−10 yr. Investigations of the collapse of the central California fishery have focused on changes in oceanographic conditions that may affect survival of eggs and larvae (Wild 1980) and a nemertean worm that preys on crab eggs (Wickham 1979). The cyclic phenomenon in northern California has been examined for oceanographic influences (Botsford and Wickham 1975; Peterson 1973) and density-dependent mechanisms (Botsford and Wickham 1978; McKelvey et al. 1980). One of the limitations inherent in all of the above studies is the lack of estimates of recruitment to the crab population.

Limited tagging studies (Cleaver 1949; Jow 1965) and catch per unit of effort (CPUE) analysis (Gotshall 1978a) indicate that about 85% of the available male crabs are harvested each year. The legally available crabs are males greater than 159 mm carapace width (about 3−4 yr old). This high exploitation rate has led to the assumption that each year's catch is an adequate estimate of the preseason abundance of the legal male Dungeness crabs (Botsford and Wickham 1975, 1978; Peterson 1973; Wild 1980). Unfortunately, none of the tagging or CPUE studies were conducted in years of increasing crab catch during which the fishery's capacity may have been insufficient to maintain the high exploitation rate achieved in other years. We utilize here a Leslie analysis (Leslie and Davis 1939; Ricker 1975, p. 150) of the decline in CPUE in each fishing season to estimate preseason abundance, then examine the time series of annual exploitation rates in the Dungeness crab fishery.

Methods

Our analysis is based on fishery catch statistics collected by the California Department of Fish and Game (Annual Market Crab Statewide Reports 1951−77). These include total catch, C_i, and total number of deliveries (landings), E_i, stratified by month, i, and statistical region (Fig. 1). We consider region 2A in northern California and 1B in central California because they account for most of the catch. In each month we calculate two variables:

$$\text{catch per unit of effort} = \text{CPUE}_i = C_i/E_i$$

$$\text{cumulative catch} = K_i = \sum_{j=1}^{i-1} C_j + 0.5{*}C_i.$$

According to Leslie's method, CPUE should decline linearly with increasing cumulative catch. We calculate a linear, least-squares regression of CPUE on K using monthly data in each year and region. Because the entire population would have been captured if CPUE were reduced to zero, the K axis intercept is interpreted as the abundance at the beginning of the fishing season, N_0. A 95% confidence limit on N_0 is calculated according to Ricker (1975). The annual exploitation rate, H, is defined as the ratio of total annual catch to N_0.

Some data selection was necessary to equalize the precision of data within a year and to eliminate data that were obviously biased by recruitment. Data based on few deliveries are not precise and are typically at nearly the same value of cumulative catch as data from adjacent months. Therefore, when fewer than 20 deliveries were made in the first calendar month of the season, data from that month were combined with data from the following month. Effort was greatly reduced during the summer in northern California so data from June, July,

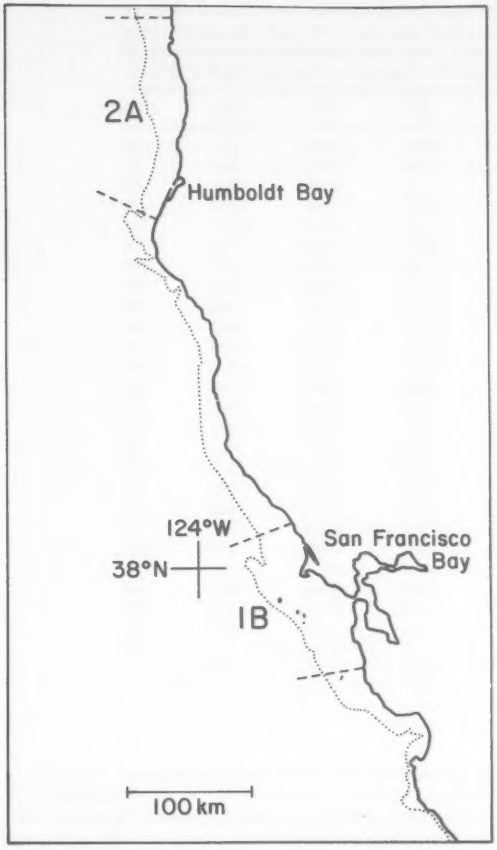

FIG. 1. Map of California coast showing statistical regions 1B and 2A used in this study. Dotted line is the 100-fath. (183 m) isobath.

and August were combined into one value for the Leslie analysis.

Small crabs that molt during the fishing season and are recruited to the fishery should not be included in the analysis because they violate the assumption of a closed population. In northern California most male crabs molt during late summer and autumn. The season is closed during this period to prevent fishing on recently molted soft crabs. Because few males molt during the fishing season there will be little recruitment to the stock of legal size males within the season. In central California molting occurs earlier in the summer, and CPUE increased in June and July (Table 1). We interpret this as recruitment to the fishable population and excluded June and July from the analysis for central California.

Results

The trend in CPUE relative to cumulative catch exhibited four basic patterns. The first pattern was a linear trend with negative slope (Fig. 2A). Years with this pattern conform well with the assumptions of the Leslie method, have a high correlation coefficient, and are usually associated with a high exploitation rate. The years 1951–56 in central California typify this pattern. In the second pattern, CPUE is moderately high in the first month then declines to a low and rather constant level for the remainder of the season (Fig. 2B). In these years the total catch was low and most of it was taken in the 1st month of the season. A breakdown of catch by weekly periods would have improved the precision of the Leslie analysis of these years. The third pattern is basically a linear trend with negative slope but with a large positive deviation in April or May (Fig. 2C). This pattern occurred several times in northern California (Table 1). We do not know if the deviation was caused by changes in availability of the fishable population of legal crabs or recruitment of recently molted crabs to the population. The fourth pattern, high CPUE throughout the season, occurred in 1957 and 1977 in northern California (Fig. 2D) and to a lesser degree in 1966 and central California in 1957.

TABLE 1. Ratio of catch per delivery in indicated month to catch per delivery in previous month. Months with fewer than 20 deliveries were excluded from the analysis.

	Central California		Northern California	
Month	*N* yr	Median	*N* yr	Median
Dec.	27	0.57	1	—
Jan.	27	0.72	22	0.79
Feb.	27	0.86	26	0.84
March	26	0.65	27	0.84
April	26	0.99	27	0.93
May	24	1.11	27	1.05
June	13	1.44	27	0.70
July	5	1.83	17	0.78
Aug.	0	—	5	0.87

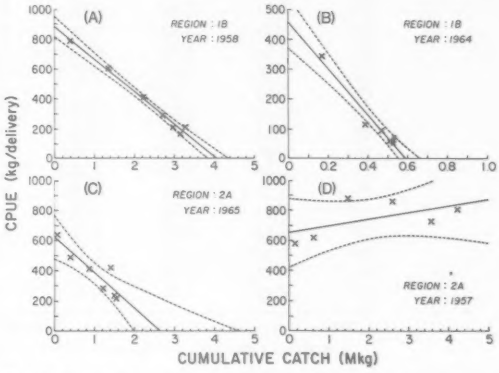

FIG. 2. Examples of relation between catch per delivery and cumulative catch. Points are monthly data. The regression line is solid and the 95% confidence limits are represented by broken lines. (A), normal year; (B), low catch year; (C), positive deviation in April–May; (D), anomalous year with high, saturated CPUE.

TABLE 2. Results of Leslie analysis for the central California Dungeness crab fishery. Catch and initial abundance, N_0, values are in megakilograms. H is the annual exploitation rate. CPD_i is the zero catch intercept of the regression of catch per delivery on cumulative catch. CPD_f is the regression estimate of catch per delivery in the final month of the fishing season. NS indicates that regression was not significant at 5% level.

Yr	Catch	N_0	95% C.I. on N_0		H	r^2	CPD_i	CPD_f
51	1.59	1.74	1.65	1.85	0.914	0.983	547	51
52	1.33	1.38	1.31	1.48	0.959	0.974	648	31
53	1.78	1.90	1.81	2.01	0.937	0.982	719	50
54	1.68	1.84	1.77	1.92	0.915	0.991	613	55
55	1.77	1.92	1.84	2.02	0.920	0.987	722	60
56	2.16	2.42	2.31	2.55	0.895	0.989	768	84
57	4.05	6.19	4.96	9.51	0.654	0.849	717	252
58	3.35	4.07	3.84	4.35	0.824	0.988	884	171
59	2.27	2.60	2.49	2.74	0.874	0.987	784	104
60	2.17	2.82	2.27	4.89	0.770	0.780	644	163
61	1.04	1.27	1.18	1.40	0.822	0.968	403	73
62	0.31	0.44	0.38	0.53	0.723	0.930	215	61
63	0.64	0.74	0.70	0.79	0.868	0.977	353	48
64	0.53	0.59	0.55	0.65	0.890	0.957	457	51
65	0.34	0.46	0.40	0.63	0.741	0.859	273	71
66	0.20	0.27	0.23	0.46	0.753	0.747	259	65
67	0.18	0.25[b]	—	—	0.720[a]	0.116 NS	225	122
68	0.46	0.54	0.52	0.58	0.843	0.980	600	96
69	0.38	0.50	0.43	0.73	0.749	0.828	398	101
70	0.66	0.90	0.76	1.25	0.738	0.855	588	157
71	0.29	0.46	0.33	3.12	0.638	0.697	349	127
72	0.14	0.26	0.19	0.85	0.536	0.678	201	95
73	0.13	0.18	0.16	0.24	0.720	0.884	240	68
74	0.18	0.27	0.20	0.95	0.671	0.740	317	105
75	0.10	0.17	0.11	9.26	0.558	0.575	205	96
76	0.14	0.20[b]	—	—	0.720[a]	0.004 NS	211	192
77	0.28	0.44	0.35	0.75	0.648	0.786	316	112

[a]Mean H from years following decline in catch.
[b]Calculated from catch and mean H.

The results of the Leslie analysis are presented in Tables 2 and 3. The temporal pattern of annual exploitation rate, H, differs between the two regions. In central California, H was 92% per year during 1951–56 but declined to 72% following the collapse of the fishery. In northern California H has varied with the 10-yr cycle of catch. During the latter portion of each high catch period H has averaged 69%. In the 1st year of low catch H increased to 84%. During the remaining low catch years and the first high catch year H decreased to 54%, but the analysis did not produce a significant result in several of these years. During the second high catch year (particularly 1957 and 1977) H was indeterminately low because CPUE remained high throughout the year.

EVALUATION OF ASSUMPTIONS

Four assumptions of the Leslie analysis are that there is no natural mortality, no immigration or emigration, no recruitment, and a proportional relation between CPUE and population abundance.

The natural mortality rate of unexploited male Dungeness crab has been assumed to be about 20% per year (Botsford and Wickham 1978; McKelvey et al.1980). If this mortality is evenly distributed through the year, then the natural survival rate will be 93% during the 4-mo major fishing season. We assume that this small amount of natural mortality has a negligible effect on the results of this study.

Migration studies based on crabs tagged in northern California (Gotshall 1978b) indicate that male crabs tend to move north and offshore during late summer to early winter and south and onshore during late winter and spring. Fishing effort also moves offshore in winter and onshore in spring and summer (Gotshall 1978b), and the data do not indicate that the crabs migrate completely out of the ranges of the fishery. However, the fishery may not always be coincident with the major concentrations of crab. The April–May increase in CPUE could be a result of increased offshore winds in March forcing fishermen inshore before most male crabs moved inshore.

Recruitment to the legal male stock during the fishing season probably was small because most males molt in late summer or early autumn. However, in central California the months June and July exhibited evidence of recruitment and were excluded from the analysis. The increase in CPUE during April–May in northern California could have been caused by recently molted crabs.

We utilized the total number of deliveries in a month as the amount of fishing effort exerted on the population. Gotshall (1978a) used catch per trap for traps fished only 1 d as his measure of catch rate. This measure is preferable to catch per delivery but is available for only 6 yr. We also computed a Leslie analysis using catch per boat per month as a measure

TABLE 3. Results of Leslie analysis for northern California Dungeness crab fishery. See Table 2 for definition of terms.

Yr	Catch	N_0	95% C.I. on N_0		H	r^2	CPD_i	CPD_f
51	4.10	5.84	4.83	7.84	0.701	0.893	831	258
52	4.20	7.05	5.20	12.90	0.596	0.816	721	300
53	1.73	2.56	1.73	19.14	0.676	0.613	502	170
54	1.76	2.61	2.39	2.91	0.677	0.981	626	204
55	0.68	1.16[b]	—	—	0.590[a]	0.277 NS	244	192
56	3.61	8.47	5.80	20.27	0.426	0.765	683	397
57	4.49	—[d]	—	—	—	— NS	651	839
58[c]	4.13	6.45	5.22	9.29	0.640	0.918	1067	396
59[c]	5.32	8.19	5.90	27.87	0.649	0.747	1058	375
60[c]	4.59	7.23	5.40	17.98	0.634	0.786	976	363
61[c]	4.37	6.16	4.92	11.39	0.708	0.826	1074	320
62	1.41	1.52	1.40	1.71	0.929	0.941	894	74
63	0.29	0.49[b]	—	—	0.590[a]	0.233 NS	155	101
64	0.24	0.41[b]	—	—	0.590[a]	0.028 NS	173	146
65	1.54	2.63	2.00	4.63	0.588	0.817	619	257
66	4.16	—[d]	—	—	—	0.460 NS	757	474
67	4.57	8.10	5.90	20.26	0.565	0.725	859	375
68	5.08	7.13	6.03	9.51	0.713	0.893	1147	330
69	5.32	6.47	5.59	8.52	0.823	0.868	1519	276
70	6.11	8.50	7.50	10.31	0.719	0.953	1221	349
71	3.27	4.35[b]	—	—	0.750[a]	0.681 NS	948	367
72	1.07	1.18	1.05	1.50	0.907	0.842	694	75
73	0.48	0.82[b]	—	—	0.590[a]	0.493 NS	221	95
74	0.15	0.24[b]	—	—	0.590[a]	0.243 NS	133	98
75	0.63	1.25	0.88	3.89	0.503	0.769	281	143
76	7.14	13.75	10.73	21.37	0.519	0.872	766	375
77	11.32	—[d]	—	—	—	— NS	326	865

[a]Interpolated from years at similar portions of catch cycle.
[b]Calculated from catch and interpolated H.
[c]First month excluded from analysis because CPUE was low.
[d]Not estimated because CPUE remained high throughout season.

of catch rate. Catch per boat per month could be more appropriate than catch per delivery because in principle it is sensitive to changes in duration of gear deployment per delivery. The results were similar to, but less precise than, the results presented here.

Several factors may influence the linear relation between catch per delivery and crab abundance, especially at extremes of crab abundance. Traps, boats, and processing facilities can be saturated when crab abundance is high. These factors place an upper limit on catch per delivery; a limit which was certainly reached in 1957 and 1977. Abundance will be overestimated, hence H will be underestimated in years in which catch rate is saturated at the beginning of the season.

At low abundance each delivery may represent a greater amount of fishing effort. Deploying traps longer and not selling small catches will contribute to this bias. Gotshall (1978a) presents evidence that traps are fished longer later in the season and that catch per trap increases with increasing duration of deployment. However, examination of his data indicates that the increase in catch with increasing duration of deployment was small. From data in Gotshall's Table 2 catch per trap for traps fished 2 d appears to be greater than the 1-d catch rate by a factor of only 1.106. The 3- to 5-d catch rate was 1.322 times greater than the 1-d catch rate.The effect of this mechanism is that at low crab abundance near the end of the season, catch per delivery is a positively biased estimate of crab abundance. This causes an underestimate of exploitation rate, especially in years of low preseason abundance.

Discussion

The results obtained here significantly enhance our knowledge of recruitment and effort in this fishery. The commonly held view that catch is a high, fairly constant fraction of abundance each year, and therefore a good index of abundance and recruitment, is no longer tenable (Fig. 3). Annual exploitation rate is lower and more variable than previously thought and appears to change in a regular fashion. The pattern of H in northern California seems to be a specific response to change in abundance that repeats itself through each of the three observed cycles.

In years for which comparisons can be made, our results regarding exploitation rate H are similar to the results obtained by other authors. Gotshall (1978a) performed a Leslie analysis for the fishing seasons 1967–72 in northern California. He used catch per trap for traps fished 1 d as a measure of catch rate. In the current study the mean H for 1967–70 and 1972 (our estimate in 1971 was not significant) was 0.745. The mean H for the same 5 yr in Gotshall's study was 0.748. Both estimates exhibited an increasing trend during 1967–69 (later years of a high catch period). Gotshall (1978a) suggests that H increases during high catch years

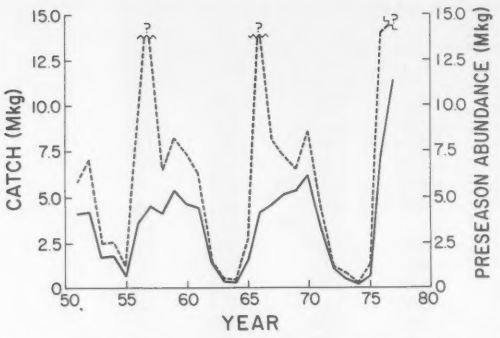

FIG. 3. Catch (solid) and preseason abundance (broken line) in the northern California Dungeness crab fishery.

because of the increasing number of boats in the fishery. He further suggests that H remains high as the population begins to decline because the boats do not immediately leave the fishery. Our study indicates that this pattern in H has recurred throughout the recent history of the northern California Dungeness crab fishery. This lagged response of fishing effort to changes in catch is being explored in more detail by L. W. Botsford, R. D. Methot Jr., and W. E. Johnston (unpublished data).

Jow (1965) examined tag recovery data in the 1963 season and estimated that 85% of the available crabs were harvested. The Leslie analysis was not significant in 1963, the second low catch year of that cycle, so a direct comparison to Jow's result cannot be made. The estimate of H by the Leslie analysis in 1962 was 92%. In other low catch years H was less than 85% but may have been underestimated because of biases in catch per delivery as a measure of crab abundance.

McKelvey et al. (1980) estimated preseason abundance in the fishery by assuming that annual fishing mortality rate was proportional to the total number of traps in the fishery. Their estimate of the constant of proportionality relating mortality rate to the number of traps was based on the 6 yr analyzed by Gotshall (1978a). Neither variable exhibited its full range during that period. They propose that fishing mortality rate (and annual exploitation rate) has increased as the number of traps in the fishery has increased. Our estimates of preseason abundance indicate only a small increase in H during the period from 1951 to 1977. Some of the effect of the increase in number of fishing units was probably a concentration of effort into the beginning of the season rather than an increase in fishing mortality throughout the season.

The previously assumed high constant exploitation rate (Peterson 1973; Botsford and Wickham 1978; Wild 1980) would imply that catch is a good index of abundance and, because there will be little escapement from the fishery, a reasonable index of recruitment. From this one would conclude that recruitment was a smooth cyclic function with gradually increasing amplitude.

The new estimates of yearly abundance discount the assumption of high, fairly constant exploitation rate. This changes our view of the relationship between fishing effort and the population and, because exploitation rates are often lower than previously believed, weakens the relationship between preseason abundance and recruitment. The implied higher escapement means that estimating recruitment from preseason abundance will require much more knowledge of natural mortality and growth rates. The new time series of preseason abundance is much less smooth than the time series of catch. Because high escapements distribute a year-class's contribution to the fished population over several years, the time series of recruitment is likely to be even less smooth than the time series of preseason abundance.

A significant finding of our study is the evidence that large year-classes occasionally dominate the fishery. In two years, 1957 and 1977 in northern California, CPUE remained high throughout the season. A similar, but less extreme, pattern occurred in 1966 and in central California in 1957. The initial abundance of crabs in these seasons must have been great to saturate CPUE throughout the season. Probably only a small fraction of the available crabs were harvested in 1957 and 1977. Very abundant single year-classes could have produced the observed pattern. Fast-growing individuals would have entered the fishery and caused the increased catch in 1956 and 1976. Most individuals would have grown to legal size the next year and saturated the fishery in 1957 and 1977.

We cannot determine how long these large year-classes continued to contribute substantially to the fishery, but the size distributions of male crabs[2] indicate substantial escapement during each of the first few years of each high catch period. Prior to the 1974 and 1975 low catch seasons the mean size of crabs larger than the legal size of 159 mm was 166 and 165 mm, respectively. Prior to 1976, the first high catch season, the mean size increased to 174 mm. Prior to 1977 the mean was 183 mm and prior to 1978 the mean was 186 mm. During previous high catch periods less information is available. Mean size increased from 173 to 182 mm during 1965–67, the first 3 high catch years of that cycle, then declined to 173–178 mm during 1968–70. Prior to 1959, the fourth high catch season, the mean size was 183 mm. These data indicate substantial escapement and suggest that a single year-class may dominate the fishery for several years, but not for the entire 6-yr high catch period.

The presence of extremely abundant year-classes seems to increase the likelihood that an environmental phenomenon is at least partly responsible for the cycles in the northern California Dungeness crab catch. Several authors (Botsford and Wickham 1975; Peterson 1973; Wild 1980) have examined the correlation between crab catch and various environmental variables. In these studies each year's catch was tacitly assumed to be composed of individuals from only 1 year-class. Therefore, computed correlation between consecutive catches would be interpreted as similarity in the environmental conditions which produced the 2-year-classes rather than as a single year-class contributing to the fishery for 2 yr. By re-examining the relationship between environmental factors and these revised estimates of recruitment, we expect to

[2]Unpublished data from preseason surveys conducted by the California Department of Fish and Game. Data are on file in Menlo Park, CA. Results from 1970s are summarized here with permission of R. Warner, from the California Department of Fish and Game, Eureka, CA.

elucidate further the possible causes of the cycles in catch of Dungeness crab in northern California.

Acknowledgments

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Seasonal Variation in the Chemical Composition and Condition Indices of Pacific Oyster, *Crassostrea gigas*, Grown in Trays or on the Sea Bed

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WHYTE, J. N. C., AND J. R. ENGLAR. 1982. Seasonal variation in the chemical composition and condition indices of Pacific oyster, *Crassostrea gigas*, grown in trays or on the sea bed. Can. J. Fish. Aquat. Sci. 39: 1084–1094.

Chemical composition and condition indices of tray and bottom-cultured Pacific oyster, *Crassostrea gigas*, were measured and compared over a 13-mo period. Tray oysters were less dense than bottom oysters as a result of increased porosity of shells. Dry meat condition indices were slightly higher in oysters grown in trays. Chloride and iodide levels peaked in early spring. Minor seasonal deviations occurred from the mean 61.0% polymeric matter, 31.5% hydrophilic matter of low molecular weight, and 7.5% lipid matter in both groups of oysters. Nonprotein to protein nitrogen ratio in tray and bottom oysters averaged 0.37 and 0.35, respectively, throughout the season. A procedure was developed to assess glycogen in situ in polymeric material fractionated from meat. Glycogen averaged 79.5 and 79.0% of the total glucose in tray and bottom oysters, respectively; the remainder consisted of the homologous series of α(1→4)-linked D-glucose oligomers. Degree of polymerization of oligosaccharides in tray and bottom oysters averaged 2.93 and 2.91, respectively. Dry meat condition indices correlated predominantly with protein condition indices, only secondarily with glycogen condition indices and insignificantly with the remaining constituent condition indices of tray and bottom oysters.

Key words: *Crassostrea gigas*, tray and bottom cultures, chemical composition, nitrogen, carbohydrates, halides, density, condition indices, seasonal variations

WHYTE, J. N. C., AND J. R. ENGLAR. 1982. Seasonal variation in the chemical composition and condition indices of Pacific oyster, *Crassostrea gigas*, grown in trays or on the sea bed. Can. J. Fish. Aquat. Sci. 39: 1084–1094.

La composition chimique et les indices de condition d'huîtres (*Crassostrea gigas*) élevées sur plateaux et sur le fond ont été déterminés et comparés pendant une période de 13 mois. Par suite d'une plus grande porosité des coquilles, les huîtres de plateau sont moins denses que celles de fond. Les indices de condition des chairs sèches sont légèrement supérieurs chez les premières. Les niveaux de chlorures et d'iodures atteignent un sommet au début du printemps. Il se produit des variations saisonnières mineures par rapport à la moyenne de 61,0 % de matières polymères, de 31,5 % de matières hydrophiles de faible poids moléculaire et de 7,5 % de matières lipidiques chez les deux groupes d'huîtres. Les rapports azote non protéique/azote protéique, au cours de la saison, sont en moyenne de 0,37 et 0,35 chez les huîtres de plateau et celles de fond respectivement. Nous avons mis au point une méthode d'évaluation in situ du glycogène des matières polymères isolées des chairs par fractionnement. Le glycogène représente en moyenne 79,5 et 79,0 % du glucose total chez les huîtres de plateau et celles de fond respectivement, la balance étant constituée par les séries homologues des oligomères de D-glucose lié à α(1→4). Le degré de polymérisation des oligosaccharides chez les huîtres de plateau et celles de fond sont en moyenne de 2,93 et 2,91 respectivement. Les indices de condition des chairs sèches sont fonction surtout des indices de condition protéiques; de façon secondaire seulement des indices de condition gly-

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cogéniques et très peu des indices de condition des autres constituants chez les deux groupes d'huîtres.

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THE Pacific oyster (*Crassostrea gigas*) which was introduced into British Columbia as seed stock from Japan in about 1912 replaced the native oyster (*Ostrea lurida*) and the previously imported Atlantic oyster (*C. virginica*) as the commercially cultured species. Although considerable biological data are available on *C. gigas* in British Columbia (Quayle 1969), the only study of biochemical composition was conducted on shucked, washed specimens which suffered significant compositional change as a result of bleeding and leaching (Tully 1936).

Quality and quantity of oyster meat reflects marketable value to commercial growers. High-quality meat from "fat" oysters is usually plump, creamy white, and generally fills the shell cavity, whereas low-quality meat is translucent, shrunken in the shell, and has a relatively high water content. Hydrographic conditions, breeding cycle, and available food supply affects condition which can be measured chemically or physically. Content of solids in oyster meat has been used as a more objective assessment of condition (Engle 1958; Shaw 1961). More definitive methods compare yield of meat with maximum possible size of the meat as indicated by volume of the shell cavity as it is presumed the oyster grows its shell to accommodate the body when at its largest. The dry meat condition index (Grave 1912 and modified by Higgins 1938) is the ratio of dry weight of meat to volume of the shell cavity of the oyster times 100 or 1000 (Medcof and Needler 1941). Variations such as wet meat index (Chew et al. 1965) and meat volume index (Grave 1912) have been used, but fluctuations tend to be minimized by the high moisture content of the body meat (Shaw et al. 1967). Glycogen content is considered a precise measure of condition with presence or absence ascribed to the degree of "fatness" of the oyster (Engle 1950). Correlations have been demonstrated between dry meat condition index and glycogen content of the European oyster *Ostrea edulis* (Walne 1970; Gabbott and Stephenson 1974).

Aims of this study were to acquire an initial data base of physical and chemical parameters of oysters grown intertidally (sea bottom culture) and totally submerged (tray culture) for future comparative studies of culture areas, and to identify components of oyster meat suitable as indicators of quality.

Material and Methods

Tray- and bottom-cultured oysters of similar size were transplanted from the same location to Kuper Island in May 1980. Tray-cultured oysters were then collected from depths of 1−2 m below the surface at monthly intervals from June 1980 to June 1981, inclusively. Simultaneously at this location bottom oysters were collected from the intertidal zone. Specimens, minimum of 30 from each group, in plastic bags were transported on ice in coolers to the Fish Inspection Laboratory in Victoria, then air-freighted to the Vancouver laboratory for a maximum elapsed time of 48 h between collection and sample preparation.

Specimen Preparation and Physical Parameters

Length (anterior−posterior), width (dorsal−ventral), and thickness of each oyster were measured on a measuring board. Oysters, in the cold room, were freed from extraneous epifauna, rinsed in cold water to remove mud, drained for 5 min, then weighed. Total volume was measured by displacement. After opening the oyster at the hinge, without puncturing the body, the shell cavity fluids were drained for 5 min, the adductor muscle cut, and the meat collected in a beaker held in ice. Combined meat was weighed, homogenized anaerobically for 3 min using a Brinkman Polytron, the homogenate divided into two zip-lock bags, and frozen at −40°C. The content of one bag was freeze-dried to provide percentage dry weight or solids content of the meat. The volume of remaining shells was measured by displacement; subtraction of this value from total volume provided cavity volume. Shells drained for 5 min were weighed then dried to constant weight at 105°C to yield percentage moisture. Dry meat condition index was the ratio of freeze-dried meat (g) to the cavity volume (mL) per oyster times 1000; constituent dry weight (g) inserted into this formula gave chemical constituent condition index. Density ($g \cdot cm^{-3}$) was the ratio of weight to volume of wet whole oyster or wet shell.

Extraction of Lipid, Hydrophilic, and Polymeric Fractions

Frozen homogenized oyster meat (25 g) was weighed into a 250-mL beaker, 30 mL methanol and 125 mL of a mixture of chloroform:methanol:water (2:4:1; v/v) added, and the mixture homogenized with a Brinkman Polytron for 1 min. Following centrifugation at 10 000 rpm for 10 min, the centrifugate was removed and the residue extracted with a further 125 mL of solvent mixture. The extraction was repeated twice to yield 530 mL of solvent extract which was then added to a 2-L separating funnel followed by 500 mL each of chloroform and water, and allowed to sit overnight at 1°C. The chloroform layer was separated, concentrated to a syrup, and weighed as the lipid fraction. The remaining aqueous-methanol layer was evaporated to yield a crystalline residue weighed as the hydrophilic fraction which contained non-protein nitrogenous and carbohydrate oligomers. Residual material from extraction was placed in a weighed plastic bag, mixed well with 20 mL water, frozen, freeze-dried, and weighed as the polymeric fraction containing polymeric carbohydrate as glycogen and protein.

Chemical Parameters

Ash content was determined by ignition of freeze-dried

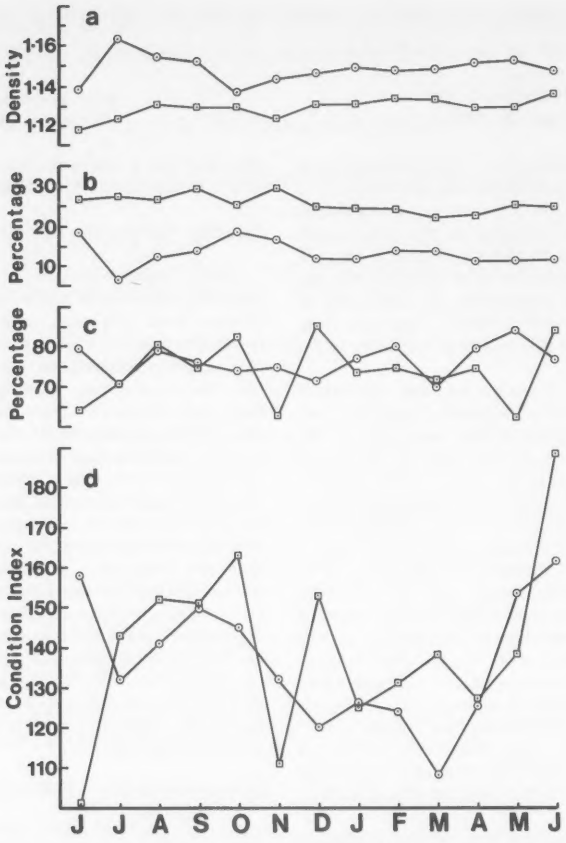

FIG. 1. Seasonal variation in (a) density of whole oyster, (b) moisture content of the shell, (c) cavity volume filled, and (d) dry meat condition index of tray- (⊡) and bottom- (⊙) cultured oysters.

oyster meat (500 mg) in an electric muffle furnace at 550°C for 70 h and insoluble ash assessed by leaching ash contained in a 4.4-μm sinter Selas crucible with 100 mL boiling water. Chloride and iodide were determined following alkali fusion of oyster meat using an iodide-selective electrode as the equivalence-point detector in argentometric titration for chloride and as a differential potentiometer in the known-addition method for iodide (Whyte and Englar 1976, 1978). Nitrogen in whole oyster and polymeric material was determined on 25-mg dried samples using micro-Kjeldahl techniques, and values for nitrogen in the latter multiplied by 6.25 provided protein contents. Nonprotein nitrogen from components of low-molecular weight contained in the hydrophilic fraction was estimated by difference. The pH of the meat was determined after diluting 2.5 g of homogenized meat to 25.0 g.

Qualitative analyses of sugars in the oysters used paper and gas–liquid chromatography. Chromatography on Whatman No. 1 paper of deionized carbohydrate solutions used the following solvents: (A) ethyl acetate–acetic acid–formic acid–water (18:3:1:4), (B) ethyl acetate–pyridine–water (10:4:3), (C) *n*-butanol–ethanol–water (3:1:1). Sugars were detected with alkaline silver nitrate (Trevelyan et al. 1950). Acid hydrolysis of the dried polymeric and hydrophilic fractions (50 mg) employed 1 mol/L H_2SO_4 at 100°C for 16 h followed by neutralization with barium carbonate. Sugars in the hydrolyzates were identified as corresponding alditol acetates with meso-inositol as an internal standard (Sawardeker et al. 1965) by gas–liquid chromatography on columns (1.8 m × 0.32 cm) of (a) 3% Silar 10C and (b) 3% Silar 5CP on Gas Chrom Q (100–120 mesh) operating at 185 or 205°C with a nitrogen flow rate of 30 mL/min.

Quantitative analysis of polymeric carbohydrate (glycogen) in the polymeric fraction, and glucose oligomers in the hydrophilic fraction used the phenol–sulfuric acid procedure (Dubois et al. 1956) and the alkaline–copper reagent (Horwitz 1975) with D-glucose as the standard. Glycogen working solution was prepared by hydrolyzing 100 mg dry polymeric fraction with 2 mol/L H_2SO_4 at 100°C for 2 h and diluting the hydrolyzate to 100 mL for the stock solution, portions of which were filtered through Millipore glass-fiber

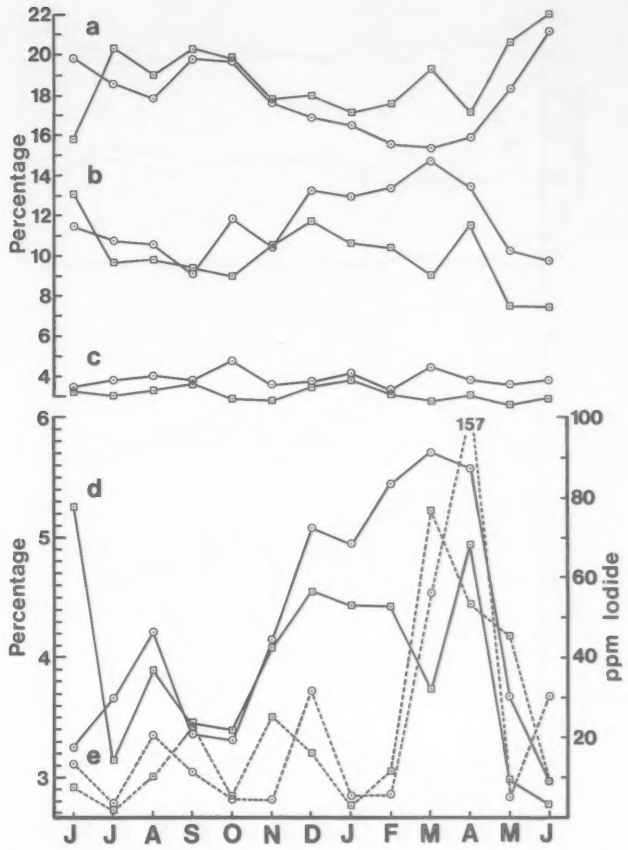

FIG. 2. Seasonal variation in content of (a) solids in wet meat and (b) total ash, (c) insoluble ash, (d) chloride, and (e) iodide (lower right scale) in dry meat from tray- (⊡) and bottom- (⊙) cultured oysters.

filters and diluted 1:25 for the phenol–sulfuric acid procedure. Glycogen values were obtained by multiplying the equivalent glucose values by 0.90. Total carbohydrate in the dried hydrophilic component was obtained by hydrolyzing 170 mg with 2 mol/L H_2SO_4 at 100°C for 2 h, diluting the hydrolyzate to 50 mL as a stock solution, filtering portions of this solution as above, and diluting to 2:100 and 10:25 as working solutions for determination by the phenol and copper reagent methods, respectively. Working solutions for alkaline–copper reagent determinations were neutralized to phenol red end point with 2 mol/L NaOH prior to final dilution. Total reducing sugar as glucose in the hydrophilic fraction was determined by the alkaline–copper reagent using a working solution of 250 mg hydrophilic fraction diluted in 50 mL water.

Effectiveness of the trisolvent extraction system to remove oligomeric carbohydrate was examined as follows. Polymeric fraction (December tray oysters, 0.4211 g) was homogenized with 250 mL of the solvent ethanol:water (4:1, v/v for 5 min using a Brinkman Polytron, then centrifuged and the centrifugate evaporated to dryness (0.0310 g, 7.36% yield). This residue was dissolved in exactly 250 mL water and a portion further diluted 1:5 to provide a working solution. Analysis by the phenol–sulfuric acid method yielded a total glucose equivalent content of 2.488 mg (0.591% of the polymeric fraction).

Results and Discussion

To minimize compositional variations resulting from size-class differences, oysters of similar size were collected and although slight monthly fluctuations were evident the overall mean sizes were comparable with dimensions for tray (n = 351) and bottom (n = 359) oysters over the 13-mo period averaging 9.88 (SD 1.20) and 10.79 (SD 1.53) cm in length, 6.30 (SD 0.79) and 6.10 (SD 1.20) cm in width, and 3.19 (SD 0.49) and 3.13 (SD 0.66) cm in thickness, respectively.

Weight and volume measurements indicated that whole

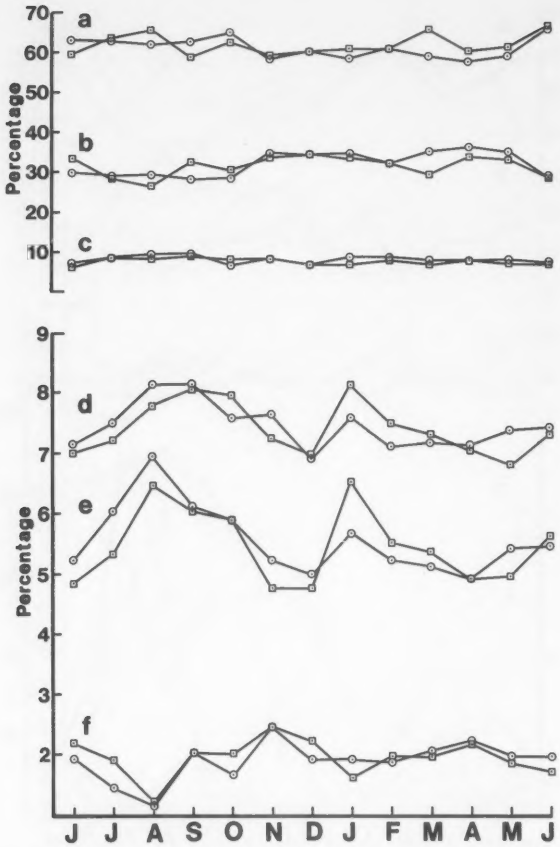

FIG. 3. Seasonal variation in content of (a) polymeric fraction; (b) hydrophilic fraction of low molecular weight; (c) lipid fraction; (d) total nitrogen; (e) polymeric nitrogen, times 6.25 as protein; and (f) nonprotein nitrogen in dry meat from tray- (⊡) and bottom- (⊙) cultured oysters.

bottom oysters were 14.9% more dense than tray oysters (Fig. 1a) as a result of the bottom shell's average density of 1.9569 $g \cdot cm^{-3}$ (SD 0.1114) compared to that of the tray shell's 1.5835 $g \cdot cm^{-3}$ (SD 0.0739). Although total average volume of shell to dry meat in the tray oyster was 8.80 mL/g compared with the bottom oyster's 7.84 mL/g, the lower density of the former reflected the more porous nature of the shell structure as evidenced by the higher moisture retention (Fig. 1b). Calcite–ostracum layers which make up the major portion of the shell are frequently interrupted by soft porous chalky deposits formed by minute crystals of calcite oriented at an angle to these subnacreous layers (Galtsoff 1964). The more porous nature of shells from tray relative to bottom oysters from other locations indicates the tendency of the totally submerged mollusk to deposit higher proportions of porous chalky material during shell growth. Deposition of shell as a function of habitat might imply that the increased protection from abrasion and desiccation required by the intertidal mollusk necessitates an increased deposition of the tougher and more impervious calcite–ostracum layers.

Seasonal average cavity volumes of tray and bottom oysters, 34.05 and 35.31 mL, respectively, were similar, but the degree to which this space was filled by meat fluctuated throughout the season (Fig. 1c). Assuming unit density for the meat, values illustrated (Fig. 1c) provide percentage cavity volume filled or represent the wet weight condition index using 100 as the multiplier. Although similar to the dry meat condition index (Fig. 1d), seasonal variations based on wet meat were less distinct, failing to illustrate chemical compositional changes, as a result of the 81.11 and 82.05% average moisture content in the tray and bottom oyster meat, respectively.

Based on dry meat condition index values (Fig. 1d), tray oysters, averaging 140 (SD 22), were generally in better condition than the intertidal mollusks, averaging 136 (SD 16), although oysters with indices above 100 are considered excel-

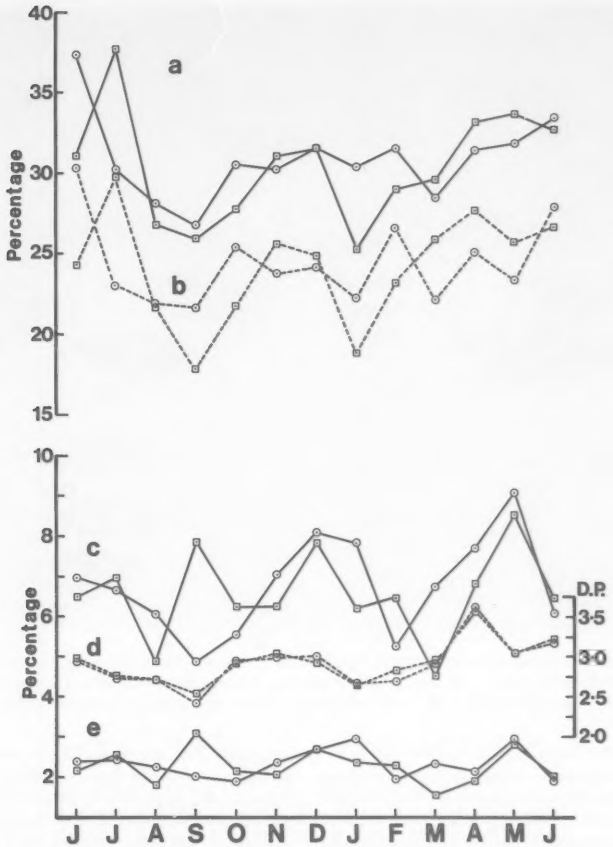

FIG. 4. Seasonal variation in content of (a) total carbohydrate as glucose; (b) polymeric carbohydrate as glucose, times 0.9 as glycogen; (c) total carbohydrate as glucose in the hydrophilic fraction (hydrolyzed oligomers); (e) total reducing carbohydrate as glucose in the hydrophilic fraction (nonhydrolyzed oligomers) — all as percentages of dry meat, and (d) degress of polymerization (D.P. right scale) of glucose oligomers in tray- (⊡) and bottom- (⊙) cultured oysters.

lent (Westley 1963). The relatively low value of 101 for the index of the tray oyster in June 1980 was considered to result from transplant stress since the following month an increase of 42 index units was observed. Values of pH, 6.41 (SD 0.08) and 6.46 (SD 0.11) for the tray and bottom oyster meat, were well above the 6.0 value at which quality of oysters is considered acceptable organoleptically (Liebman et al. 1957). Optimum physical conditioning of intertidal and subtidal oysters occurred during the summer months.

Solids in the meat of the tray oyster fluctuated over a wider range than the bottom oyster (Fig. 2a). A higher level of organic matter occurred in the tray oyster meat as illustrated by the total ash contents (Fig. 2b). Insoluble ash was more prevalent in the bottom oyster solids as would be expected from the habitat occupied (Fig. 2c). Chloride correlated well with and averaged 39.2 and 36.3% of the total ash content of tray and bottom oysters, respectively. The inverse relationship observed between chloride (Fig. 2d) and total solids in the meat (Fig. 2a) was considered a function of ionic regulation within the mollusk and the salinity of water from which the oysters were collected. Interestingly, chloride contents of tray and bottom oysters with maximum dry meat condition indices were 0.62 and 0.63 g per 100 grams wet meat, respectively, and for the lowest indices 0.83 and 0.88 g chloride per 100 grams wet meat, respectively. Regression analysis of the content of chloride in wet meat with dry meat condition index of bottom oysters indicated a linear relationship with a coefficient of correlation equal to 0.79, whereas values from tray oysters exhibited no functional relationship. This relationship between chloride and condition index will require further study as a potential quality indicator.

Fluctuations in iodide content of oyster meat (Fig. 2e)

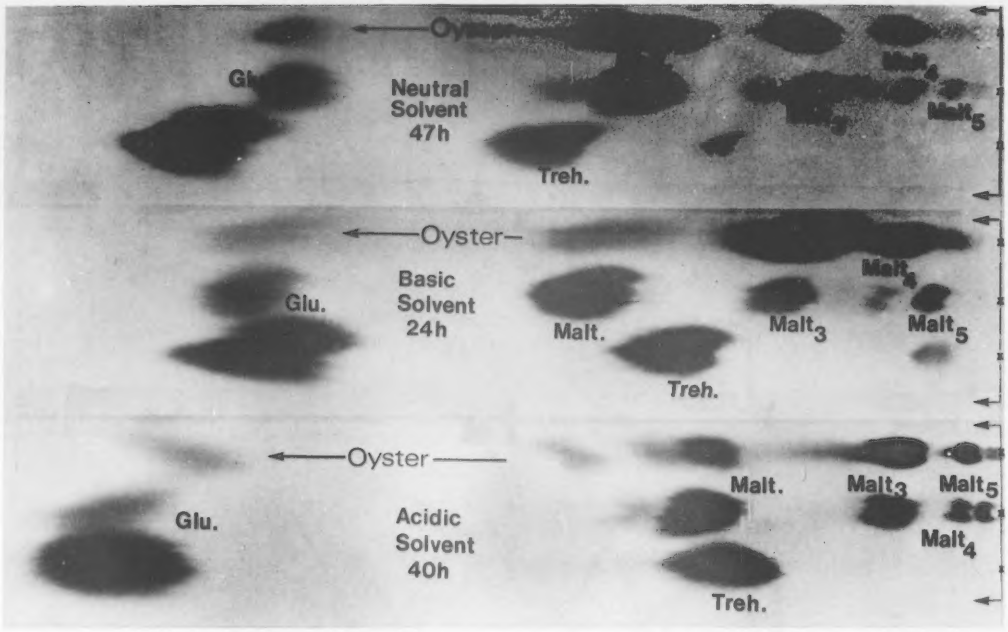

FIG. 5. Paper chromatograms of carbohydrate in the hydrophilic fraction from tray oyster meat, run in three solvent systems (see text) and visualized with alkaline silver nitrate. Glu. = glucose; Malt. = maltose, 4-O-α-D-glucopyranosyl-D-glucopyranose; $Malt_3$ = maltotriose; $Malt_4$ = maltotetraose; $Malt_5$ = maltopentaose; Treh. = α,α-trehalose, α-D-glucopyranosyl α-D-glucopyranoside.

suggested accumulation by ingestion of plankton rich in iodine or iodo-organic compounds rather than gross assimilation of this element from the seawater into the tissue which provided a base level under 5 parts per million. Involvement of food supply was substantiated by the increase in solids and dry meat condition index in the months following March–April when peak levels of iodide were observed. Oysters have been used in the past as a dietary source of iodine to overcome maladies attributed to iodine deficiency (Coulson 1933).

Trisolvent extraction initially applied to assessment of lipid in fish (Bligh and Dyer 1959) proved invaluable for analysis of chemical constituents in marine algae (Whyte and Southcott 1970; Whyte and Englar 1981) and was applied to extractive fractionation of oyster meat into lipid, hydrophilic, and polymeric components. The lipid fraction averaged 7.35 and 7.76% of the solids in the tray and bottom oyster, respectively, and exhibited insignificant seasonal fluctuations (Fig. 3c). Polymeric material as the major fraction averaged 61.37 and 60.61% of the meat from the tray and bottom oyster, respectively, and the seasonal fluctuations, varying from 57.0 to 65.5% (Fig. 3a) were mirrored in the variances observed for the hydrophilic fraction containing compounds of low molecular weight (Fig. 3b). This procedure was effective in separating for analysis the polymeric and low-molecular weight nitrogenous and carbohydrate constituents in oyster meat.

Comparable seasonal changes were observed in the total nitrogen contents of meat from tray and bottom oysters (Fig. 3d), and the respective 7.40 and 7.43% average values suggested that nutrient conditions were similar for both cultures. Polymeric nitrogen averaged 73.7 and 74.7% of the total nitrogen in the tray and bottom oyster meat and was responsible for the seasonal fluctuations in the total nitrogen (Fig. 3e). Nonprotein nitrogen in tray and bottom meat varied similarly with each month of the year (Fig. 3f) providing average values of 1.95 and 1.85%, respectively. Seasonal ratios of nonprotein to protein nitrogen, 0.37 (SD 0.09) and 0.35 (SD 0.08) for tray and bottom meat, respectively, suggested that an equilibrium in the composition of the nitrogen pool was maintained whenever possible, subject to environmental stress.

Glucose is the blood sugar in bivalve mollusks and stored glycogen in the body serves as a source of this monosaccharide (Goddard and Martin 1966). Hydrolyzates of polymeric and hydrophilic fractions of tray oysters collected in July contained 98.0 and 94.8% glucose, 0.6 and 0.8% ribose, 0.5 and 0.3% mannose, 0.4 and 2.4% galactose, 0.5 and 1.7% fucose, respectively, and 2-deoxyglucose as trace quantities in both. Glucose was therefore used as a standard in all subsequent analyses of carbohydrates.

Many difficulties surround glycogen determination using extraction, alcohol precipitation, and end product analysis (Westenhouse 1968). Glycogen is severely degraded when

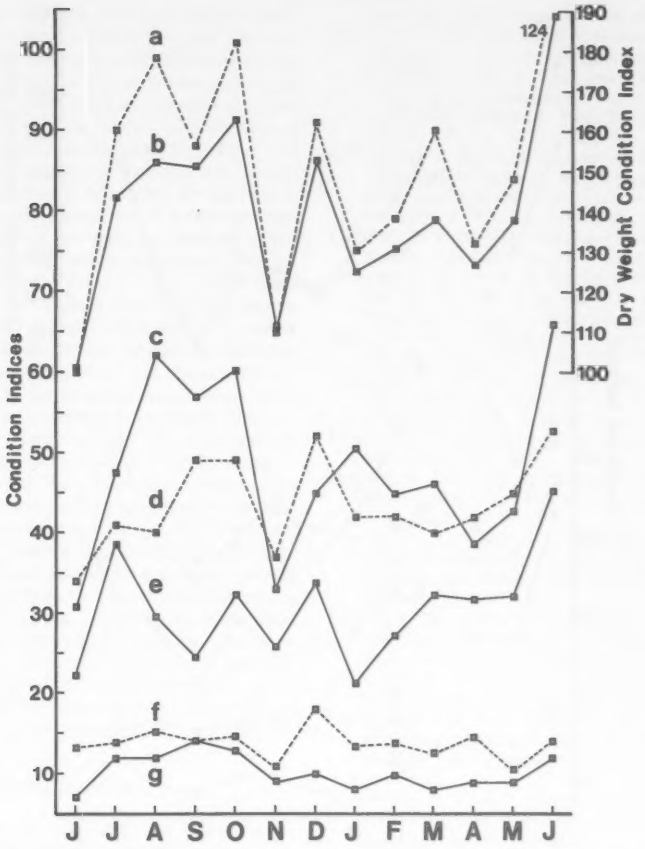

FIG. 6. Comparison of dry meat condition index (b, upper right scale) with condition indices of polymeric material (a), protein (c), hydrophilic material (d), glycogen (e), total ash (f), and lipid (g) calculated for tray-cultured oyster.

extracted with alkali, is hydrolyzed when extracted with trichloroacetic acid, and is only partially removed when extracted with water or dimethyl sulfoxide (Be Miller 1965). In addition degraded polysaccharide cannot be quantitatively precipitated from extraction solutions with alcohol (van Handel 1965). These problems were overcome by assessing the glycogen in situ in the polymeric fraction, firstly by hydrolyzing the fraction under mild conditions to ensure nondegradation of glucose (Selvendran et al. 1979), and then determining the total carbohydrate in the hydrolyzate. Lack of oligomeric carbohydrates remaining in the polymeric fraction after trisolvent extraction was verified by the isolation of only 0.59% glucose from the fraction exhaustively extracted with 80% aqueous ethanol, a solvent mixture known to segregate polymeric from oligomeric carbohydrates (Whistler and Sannella 1965). Dissolution of this carbohydrate could also have originated from physical degradation of the glycogen with the high shear homogenizer used in the verification procedure further strengthening the validity of this in situ assessment.

Total carbohydrate content obtained by summation of the glucose determined in the polymeric and hydrophilic fractions using the phenol–sulfuric acid procedure varied considerably throughout the year (Fig. 4a). These fluctuations reflected changes in the polymeric carbohydrate component (Fig. 4b) which averaged 79.5 and 79.0% of the total carbohydrate as glucose in the tray and bottom oyster meat, respectively. Overall values for total carbohydrate of the tray and bottom oyster were 30.4 and 34.0% of dry solids, respectively.

Assessment of carbohydrate in hydrolyzed and nonhydrolyzed portions of the hydrophilic fraction, with alkaline copper reagent, provided values for oligosaccharides as equivalent total glucose (Fig. 4c) and as equivalent reducing-end glucose (Fig. 4e). The ratio of these values provided the average degree of polymerization (D.P.) of the oligomeric carbohydrate contained in the oysters, and although

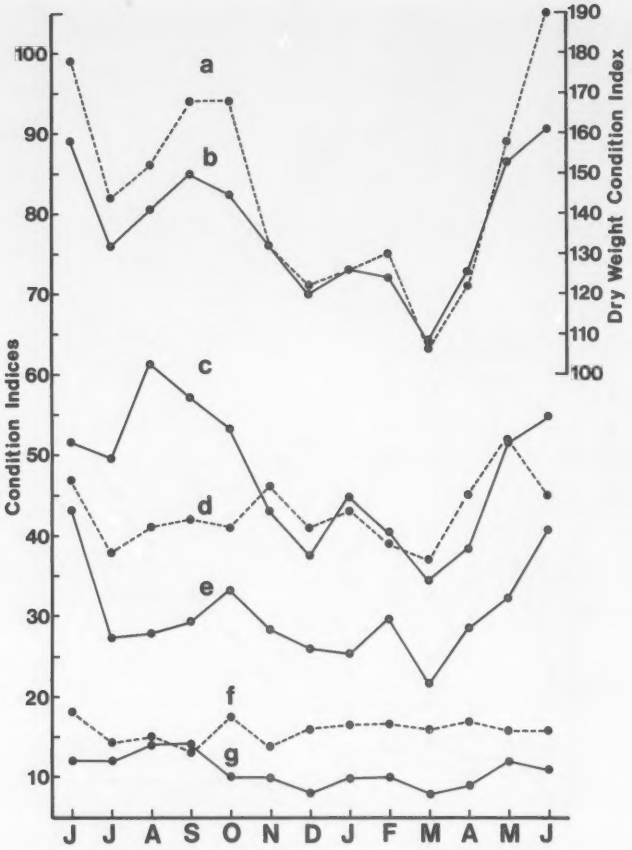

FIG. 7. Comparison of dry meat condition index (b, upper right scale) with condition indices of polymeric material (a), protein (c), hydrophilic material (d), glycogen (e), total ash (f), and lipid (g) calculated for bottom-cultured oyster.

fluctuations were evident the monthly values were virtually identical (Fig. 4d). Despite the considerable fluctuation of carbohydrate in dry meat (Fig. 4), the seasonal average D.P. of 2.93 and 2.91 for the oligomers in the tray and bottom oyster, together with the identical seasonal value of 0.27 for the ratio of oligomers to glycogen in both, indicated that an equilibrium in the composition of the carbohydrate pool of the animals was maintained whenever possible, subject to environmental influences.

Paper-chromatographic examination of the carbohydrates in the hydrophilic fraction of the tray oyster collected in July corroborated the analytical value for an average D.P. of ~ 3 (Fig. 5). The trisaccharide maltotriose formed the major component of the α-(1→4)-linked D-glucose homologous series, maltose, maltotriose, maltotetraose, and maltopentaose that occurred with only minor amounts of glucose. The occurrence of this homologous series of oligosaccharides is also in agreement with the current view that glycogen in synthesized by transfer of D-glucose residues from UDP-D-glucose via UDP-D-glucose:glycogen 4-α-D-glucosyl transferase to a $[(1\rightarrow4)\text{-}\alpha\text{-D-glucosyl}]_n$ acceptor forming an α-(1→4)-linked D-glucose primer chain. When these primer chains become about 10 residues long, they are transferred forming α-(1→6)-D-glucose linkages by an oligo-transferase enzyme (1→4)-α-D-glucan:(1→4)-α-D-glucan 6-glucosyl transferase (Hassid 1970). Under normal physiological conditions, therefore, the oyster tended to maintain these primer oligosaccharides at an average D.P. of about 3 with seasonal fluctuations perhaps indicative of environmental stress; this will be further investigated as a quality indicator.

Trehalose, α-D-glucopyranosyl α-D-glucopyranoside was not evident in the carbohydrate content of either tray- or bottom-cultured *C. gigas* (Fig. 5), although this nonreducing disaccharide, prevalent in insect hemolymph, was considered a component of *C. virginica* in amounts varying from 0.19 to 3.30 mg/g wet weight (Badman 1967).

The glycogen content of adult oysters, *O. edulis*, varied seasonally and correlated directly with the dry meat condition index (Walne 1970); however, no correlation was evident in these parameters from either the tray or bottom cultures of *C. gigas* (Fig. 1d and 4b). From July the percentage glycogen decreased to the lowest levels for the year in September, a month when tray and bottom oysters attained high dry weight condition indices. Declines in glycogen content in *C. virginica* were attributed to spawning (Engle 1950), but the considerable monthly fluctuations, particularly in bottom-cultured *C. gigas* (Fig. 4b), suggested availability of food and hydrographic conditions were of paramount importance. The significant decline in November of the dry meat condition index of the tray oyster (Fig. 1d) resulted more from low protein content (Fig. 3e) than the relatively high glycogen content (Fig. 4b), yet any correlation between percentage content of protein and dry meat condition indices was obscure. Effects of percentage constituents on condition indices were more apparent when normalized to chemical constituent indices.

Superimposition of dry meat condition indices on chemical condition indices for tray and bottom oysters (Fig. 6 and 7, respectively) illustrated that the polymeric material indices (Fig. 6 and 7a) paralleled more closely the dry meat condition indices (Fig. 6 and 7b) than indices of the hydrophilic material (Fig. 6 and 7d), the lipid material (Fig. 6 and 7g), or the total ash (Fig. 6 and 7f). Fluctuations in the polymeric material indices resulted principally from the protein condition indices (Fig. 6 and 7c), correlating closely with the dry meat condition indices, and only secondarily with the glycogen condition indices (Fig. 6 and 7e). These data suggest that although glycogen contributes to the energy requirements of *C. gigas*, its major role may lie in the interconversion of protein reserves which dictate the index of condition for this mollusk.

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Patterns of Nitrogen Excretion and Oxygen Consumption During Ontogenesis of Common Carp (*Cyprinus carpio*)

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KAUSHIK, S. J., K. DABROWSKI, AND P. LUQUET. 1982. Patterns of nitrogen excretion and oxygen consumption during ontogenesis of common carp (*Cyprinus carpio*). Can. J. Fish. Aquat. Sci. 39: 1095–1105.

By monitoring nitrogen (ammonia and urea) excretion and oxygen consumption in a continuous manner during early development (from 18 to 350 degree days) of common carp, *Cyprinus carpio*, we noted high rates of ammonia-N excretion (>100 and >50 $\mu g\ N \cdot h^{-1} \cdot 10^3$ $eggs^{-1}$) and of oxygen consumption (>1 and >2.5 $mg \cdot h^{-1} \cdot 10^3$ $eggs^{-1}$) at hatching and at the onset of free-swimming stages, respectively. There was a diurnal rhythm in metabolic activity. The relative proportions of urea-N and ammonia-N varied during early development; the mean urea-N excretion rate amounted to 21.9 ± 8.7% of total nitrogen, and there was no significant difference between embryonic and postembryonic stages. Fasted free-swimming larvae exhibited increased metabolic activity just before the onset of massive mortality (>75 $\mu g\ N \cdot h^{-1} \cdot 10^3$ $eggs^{-1}$ and >2 mg $O_2 \cdot h^{-1} \cdot 10^3$ $eggs^{-1}$ of nitrogen excretion and oxygen consumption, respectively). Ammonia excretion rates increased with temperature, the Q_{10}'s being 2.36, 2.33, and 3.53 during embryonic, hatching, and free-swimming stages, respectively.

Key words: carp, ontogenesis, nitrogen excretion, ammonia, urea, oxygen consumption, temperature, diurnal rhythm

KAUSHIK, S. J., K. DABROWSKI, AND P. LUQUET. 1982. Patterns of nitrogen excretion and oxygen consumption during ontogenesis of common carp (*Cyprinus carpio*). Can. J. Fish. Aquat. Sci. 39: 1095–1105.

En suivant de façon continue l'excrétion d'azote (ammoniac et urée) et la consommation d'oxygène durant les premières phases du développement (de 18 à 350 jours-degrés) de la carpe, *Cyprinus carpio*, nous avons pu noter des taux élevés d'excrétion de N-ammoniac (>100 et >50 $\mu g\ N \cdot h^{-1} \cdot 10^3$ $œufs^{-1}$) et de consommation d'oxygène (>1 et >2,5 $mg \cdot h^{-1}\ 10^3$ $œufs^{-1}$) à l'éclosion et au début des stades pélagiques respectivement. L'activité suit un rythme nycthéméral. Les proportions relatives de N-urée et N-ammoniac varient durant les premiers stades de développement; le taux d'excrétion moyen de N-urée représente 21,9 ± 8,7 % de l'azote total, et les stades embryonnaires et postembryonnaires ne montrent pas de différences significatives. On constate, chez les larves pélagiques privées de nourriture, une activité métabolique accrue juste avant le début de mortalités massives (>75 $\mu g\ N \cdot h^{-1} \cdot 10^3$ $œufs^{-1}$ et >2 mg $O_2 \cdot h^{-1} \cdot 10^3$ $œufs^{-1}$ d'excrétion d'azote et de consommation d'oxygène respectivement). Les taux d'excrétion d'ammoniac augmentent en fonction de la température, les Q_{10}'s étant de 2,36; 2,33; et 3,53 durant les stades embryonnaires, d'éclosion et pélagiques respectivement.

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LIPIDS, glycogen, free glucose, amino acids, and adenylic nucleotides constitute the main energy substrates in the mature teleosteen oocyte (Boulekbache 1981). In common carp (*Cyprinus carpio*), protein and lipids contribute equally as

energy sources during early development (Kamler 1976). Through measurement of oxygen consumption by embryonic and larval stages of carp, Kamler (1976) has shown the differential utilization of energy reserves during the course of development. Further, free amino acid levels decrease during early development of rainbow trout (*Salmo gairdneri*) (Zeitoun et al. 1977) and act as selective precursors of glyconeogenesis in chum salmon (*Oncorhynchus keta*) alevins (Takahashi et al. 1978). This selective protein utilization by the embryo should be manifested by increased nitrogen excretion.

Although numerous studies pertaining to nitrogen excretion patterns in growing fish have been made (Brett and Zala 1975; Kaushik 1980), such studies during embryonic development have received little attention so far. Embryonic development of teleosts is a good model for the study of such relationships as teleost eggs are cleiodic and nitrogenous wastes are easily diffused into the aquatic environment. Although permeability of ammonia through the egg membrane was not measured, evidence to date suggests that teleost eggs excrete ammonia without any special need for its detoxification (Rice and Stokes 1974).

Rice and Stokes (1974) gave special consideration to the ornithine–urea cycle enzymes during ontogenesis of rainbow trout. Besides ammonia, teleost eggs and larvae are known to excrete some urea, uric acid, and amino acids, the differences between species being in the forms and proportions of such nitrogenous metabolites (Yarzhombek and Maslennikova 1971). Sensitivity of different life stages to ammonia concentrations in water (Federov and Smirnova 1978; Rice and Bailey 1980) and the possible accumulation of lethal ammonia concentrations in relation to density of eggs in the incubators (Bailey et al. 1980) during early development of pink salmon (*Oncorhynchus gorbuscha*) are known.

To understand better the different aspects of potential endogenous nitrogen and energy metabolism, we made a continuous quantitative appraisal of the different forms of nitrogenous waste products excreted by embryos and larvae and monitored the excretory products and oxygen consumption during ontogenesis. By elucidating the relationship between metabolism and morphogenesis, we hope to define criteria for the formulation of diets for larval culture.

Materials and Methods

Carp eggs were obtained after induced fertilization at 20°C. Three batches of eggs were transferred to the laboratory for three trials conducted during May through August. Eggs were received at the eyed stage, 50°d (degree days), except for the second trial, when they were of an earlier stage (<18°d). The three trials corresponded to the three batches of eggs. During the first trial, apart from studies during embryonic and postembryonic development, we studied free-swimming larvae kept in the metabolism chambers (described below) without feeding until massive mortality occurred at about 350°d. For the second trial, the eggs obtained were at the ovular stage (18°d) and the studies were made until yolk absorption (170°d). In the third trial, urea-N excretion was also continuously measured along with ammonia excretion and oxygen consumption.

Triplicate groups of viable eggs (300–700 in number) were maintained in three glass chambers (15 mm diameter; 150 mm long; vol. 15 mL) supplied continuously with tap water at a constant flow rate of about 10 mL·min^{-1}, through an adjustable peristaltic pump. Water temperature was constant at 20.5 ± 0.5°C, except during the embryonic development in trials I and II.

The direct monitoring of ammonia or urea nitrogen concentrations in water leaving the chambers was carried out by placing an autoanalyzer (Technicon autoanalyzer I) sampling probe at the outlet of the metabolism chamber (Kaushik 1980). A pneumatically actuated six-way rotary valve, controlled by a timer, was used to sample successively in each of the three chambers and also in the overhead inflow tank. Sampling in each chamber was done for 2.5 min, followed by 2.5 min in the inflowing water. Excretion rates in each chamber were thus recorded every 15 min. Besides, sample aliquots from three other chambers were continuously drawn over periods of 24 h and collected in small containers. These cumulative samples were rotary-evaporated to known volumes for analysis of urea nitrogen and uric acid. Oxygen consumption was measured using a portable oxygen electrode (Ponselle, France).

Because water renewal was continuous in the metabolism chambers, the oxygen level was never below 7 mg·L^{-1}. Anoxia is known to initiate hatching mechanisms in teleosts (DiMichèle and Taylor 1981). During the first trial, however, we used anoxia to accelerate hatching. Because the water temperature varied, especially during studies on embryonic stages, we chose the integrative expression of age in terms of degree days (°d) starting from fertilization to facilitate comparisons. Our terminology for depicting the different

TABLE 1. Coefficients of periodic regressions of ammonia excretion during embryonic development of carp on four successive cycles of 24 h

	Day 1	Day 2	Day 3	Day 4
Coefficients				
a0	6.42525	12.36044	36.06978	53.60629
a1	4.90517	−3.47963	−11.25370	−36.52640
b1	2.66814	4.50029	−18.52112	−8.17153
a2	3.92499	2.02666	−2.07639	15.36787
b2	0.81223	−2.48014	−0.87955	7.22459
Phase angle	0.49849	2.22898	4.16639	3.36168
Semiamplitude	5.58071	5.68862	21.67205	37.42929
T_{max}	09:54	16:30	23:55	20:50

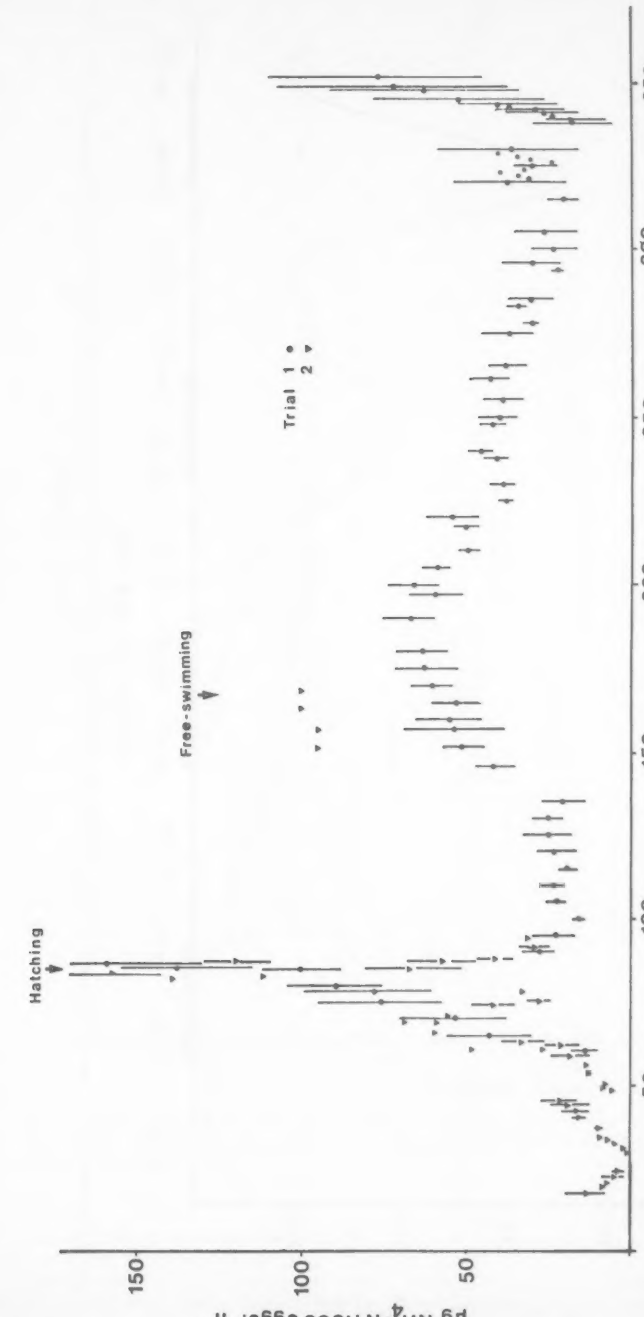

FIG. 1. Ammonia excretion rates during early development of carp. Trials I and II correspond to two different batches of eggs. For trial I, the studies were made on eggs from 50°d until massive mortality at 350°d; for the II trial, the eggs were obtained at the age of 18°d and the measurements made until free-swimming stage. The vertical bars represent standard deviations.

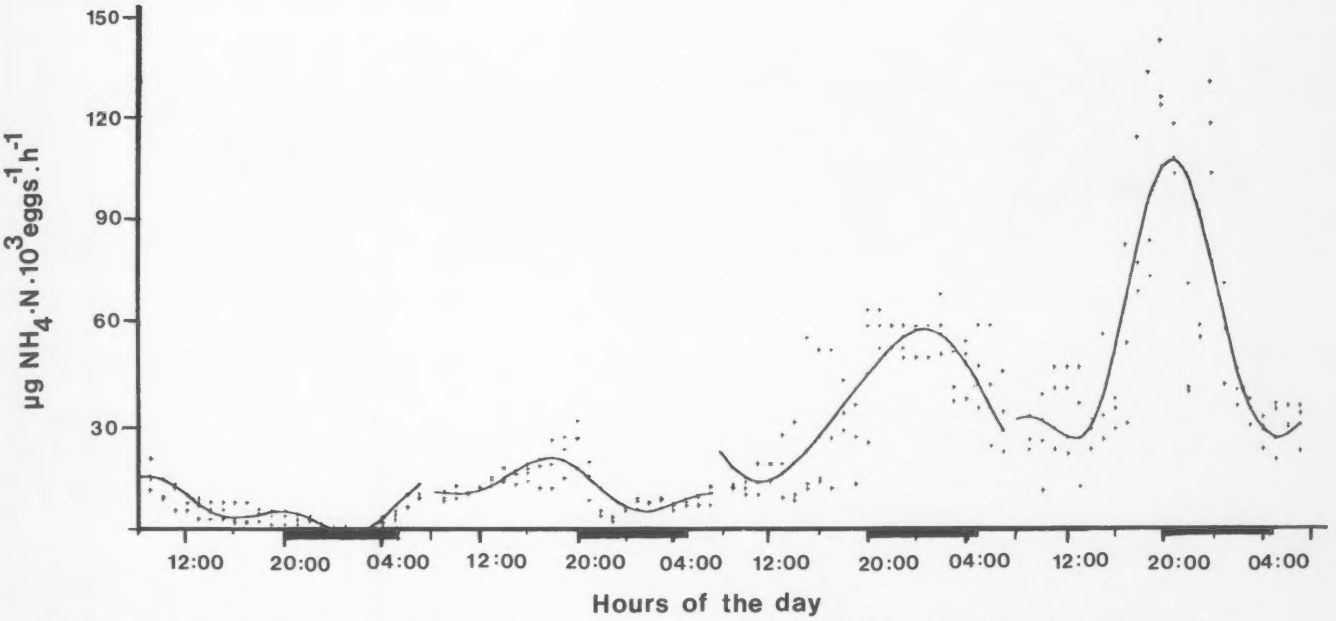

FIG. 2. Diurnal rhythm in ammonia excretion rates during 4 successive days before hatching of carp eggs. Dark periods are indicated by solid bars in the abscissa.

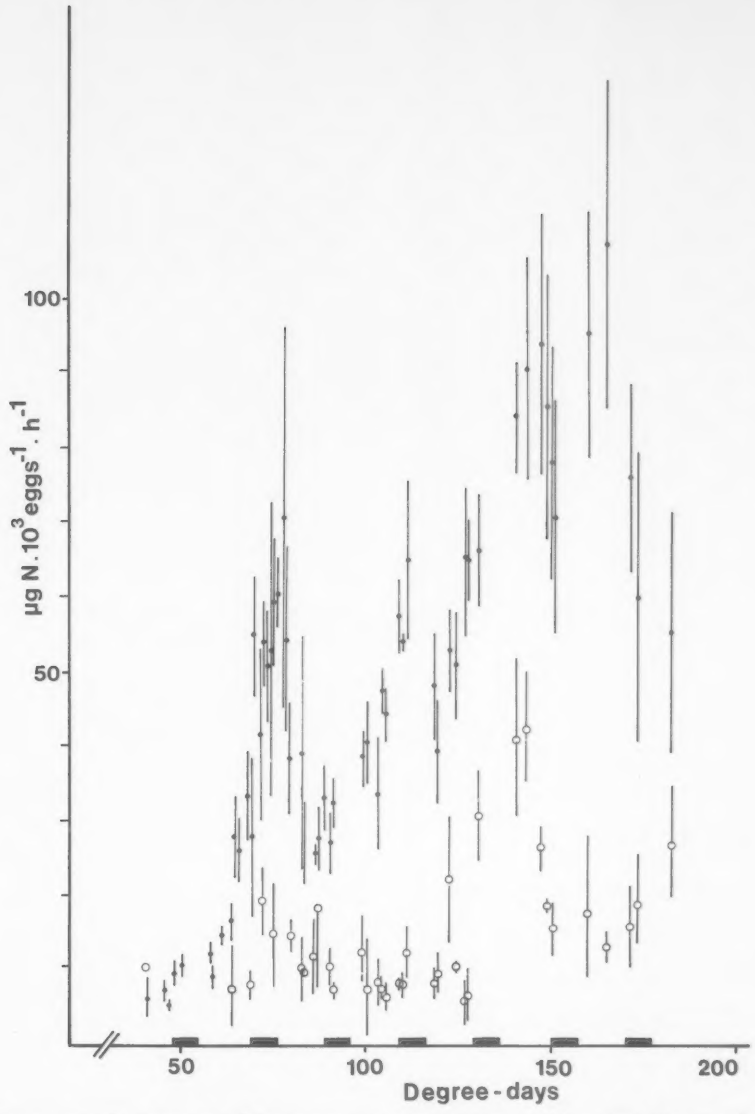

FIG. 3. Urea (○) and ammonia (●) nitrogen excretion rates until the onset of free-swimming in carp early development. The dark rectangles on the abscissa correspond to dark periods of the day. The vertical bars represent standard deviations.

developmental stages is mostly drawn from Kamler (1976).

Statistical analyses on the rhythmicity in ammonia excretion on four successive days of egg development until hatching are based on methods outlined by Bliss (1970). We calculated periodic regressions of the type

$$Y = a0 + a_i \cos(ct) + b_i \sin(ct) \ldots .$$

where $t = 0$ to $(n-1)$ number of periodic observations and $c = 2/n$, for $i = 1$ to k number of harmonics, using a program written by S.J.K. for a desk-top computer. Because of

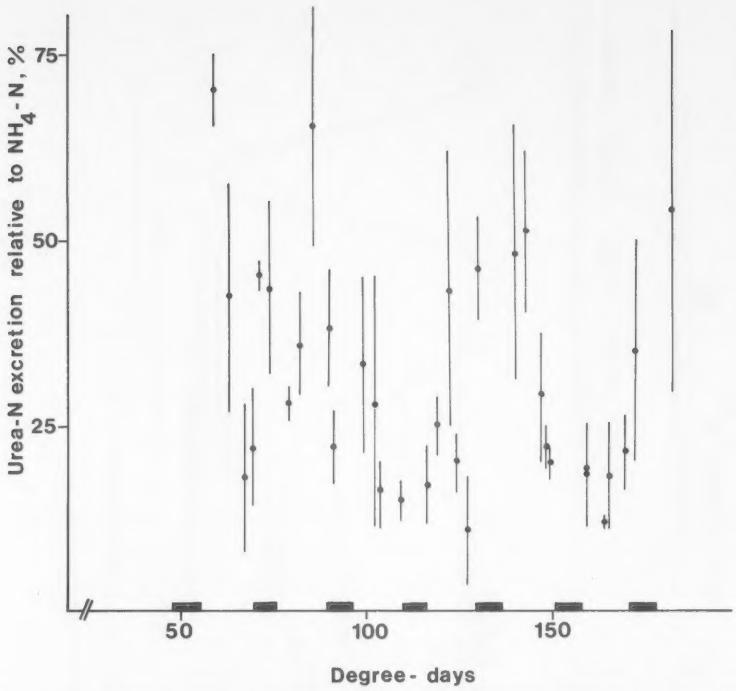

FIG. 4. Urea excretion relative to ammonia excretion during ontogenetic development of carp. Solid rectangles on the abscissa correspond to dark periods. The vertical bars represent standard deviations.

continuous monitoring of metabolic activities, cumulative results for specific periods could also be computed.

EFFECT OF TEMPERATURE

We kept triplicate groups of eggs or larvae in known volumes of water at different temperatures. They were adapted for several hours to temperatures ranging from 13 to 28°C, before being transferred to freshwater of the same temperature for the trials. We studied the influence of temperature on excretion rates at late embryonic (59°d), hatching (84°d), and free-swimming (119°d) stages, taking care to attain the same stage of development in terms of degree days at all temperatures during analyses.

Results

AMMONIA EXCRETION RATES

Three different patterns of ammonia excretion are observed during the whole course of development (Fig. 1). Between late gastrula (18°d) and midembryonic stages (around 50°d), the excretion proceeds at a very low rate (below 15 $\mu g\ N \cdot h^{-1} \cdot 1000\ eggs^{-1}$). Sporadic hatchings start occurring after 70°d in all three batches of eggs and the excretion rates start increasing by almost 10-fold. Once hatching is over, the rates decline to a level slightly higher than the prehatching levels for the next 50°d. Once they reach the larval stage (170°d), this rate once again increases to reach a level of 50 $\mu g\ N \cdot h^{-1} \cdot 1000\ larvae^{-1}$ and stays so for several hours before showing a decrease. This decline in excretion rate of fasted larvae is very slow, but as mortality sets in by 350°d, there is a sharp rise reaching levels found by end of yolk absorption.

There is a definite circadian rhythm of ammonia excretion during early development (Fig. 2). The daily ranges (twice semiamplitude) of ammonia excretion were not very different during the first 2 d (corresponding to 18–55°d), but increased considerably later on until hatching (Table 1). The time of day (T_{max}) at which the excretion rate reached a maximum varied on successive days. The analysis of variance indicated that the first two harmonics (Bliss 1970) were sufficient to describe most of the variations (≥83% of the variations were due to the two harmonics). Total ammonia-N excretion of an ontogenetic unit during embryonic, endogenous feeding or absorption of yolk (80–170°d) and during fasting is 2.35, 3.19, and 8.33 μg N, respectively (Table 2).

UREA EXCRETION RATES

Urea excretion is low during early embryonic stages, increasing twofold just before hatching (Fig. 3). This rate is

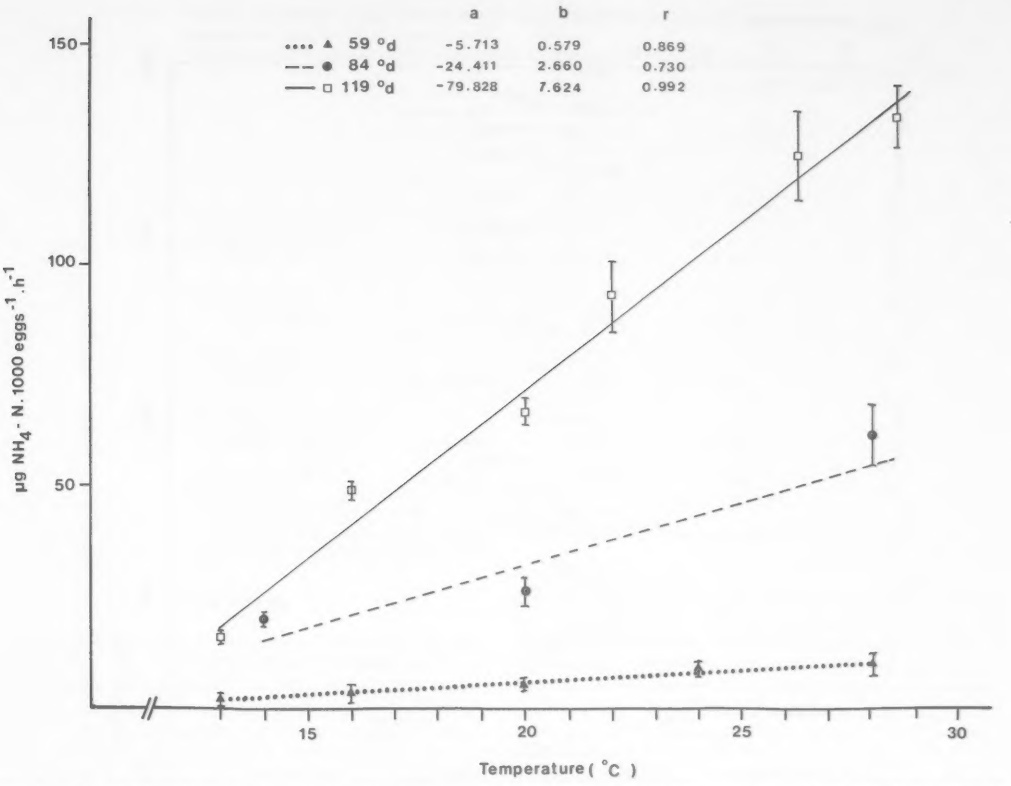

FIG. 5. Effect of temperature on ammonia excretion from carp eggs and larvae. Vertical bars represent standard deviations. Effect of temperature was studied at three different stages of development (59, 84, and 119°d).

then decreased and remains very low even after hatching, until 120°d. The peak values were noted during the protopterygiolarval stage (145°d). Figure 4 shows that urea excretion rates never went above those of ammonia excretion rates. This relative proportion of urea to ammonia (Fig. 4) also seems to show a diurnal pattern, with a decline just before dusk. The mean excretion of urea-N during the study amounted to 21.9 ± 8.7% of total (ammonia plus urea) excreted. There was no significant difference between embryonic (26.9 ± 8.9%) and larval (20.5 ± 8.2%) stages in this relative amount. Uric acid was also found to be excreted by carp larvae; however, the values were very low (below 2 µg $N \cdot h^{-1} \cdot 1000$ individuals^{-1}) during the course of development.

Effect of Temperature on Ammonia Excretion

Ammonia excretion rates are linearly related to temperature, irrespective of the stage of development (Fig. 5). Rates of ammonia excretion at 13°C in the three different stages studied were below 20 µg $N \cdot h^{-1} \cdot 1000^{-1}$. The rate–temperature relations were different at the different developmental stages. Q_{10} values calculated according to Hoar (1966) are not different between the embryonic and hatching stages, being, respectively, 2.36 and 2.33, while at the free-swimming stage, it was considerably higher (3.53).

Oxygen Consumption

Figure 6 shows that the instantaneous rate of oxygen consumption of the eggs during early and mid-embryonic stages is very low. The increase with age is gradual and by hatching, the rate is almost twice that observed at 20°d. A small decline after hatching is followed by a similar prehatching rate of increase until the end of yolk absorption (170°d) to reach a level of 3 mg. After total depletion of yolk reserves, oxygen consumption of larvae without any food declined initially by one third (240°d) to stabilize until about 300°d at a level slightly above 2 mg. High activities were shown by the time massive mortality occurred. An individual egg consumes about 0.07, 0.20, and 0.44 mg O_2 during embryonic, prelarval, and larval stages, respectively. Energy expended by an ontogenetic unit since fertilization until death is equal to 10 J (see Table 2).

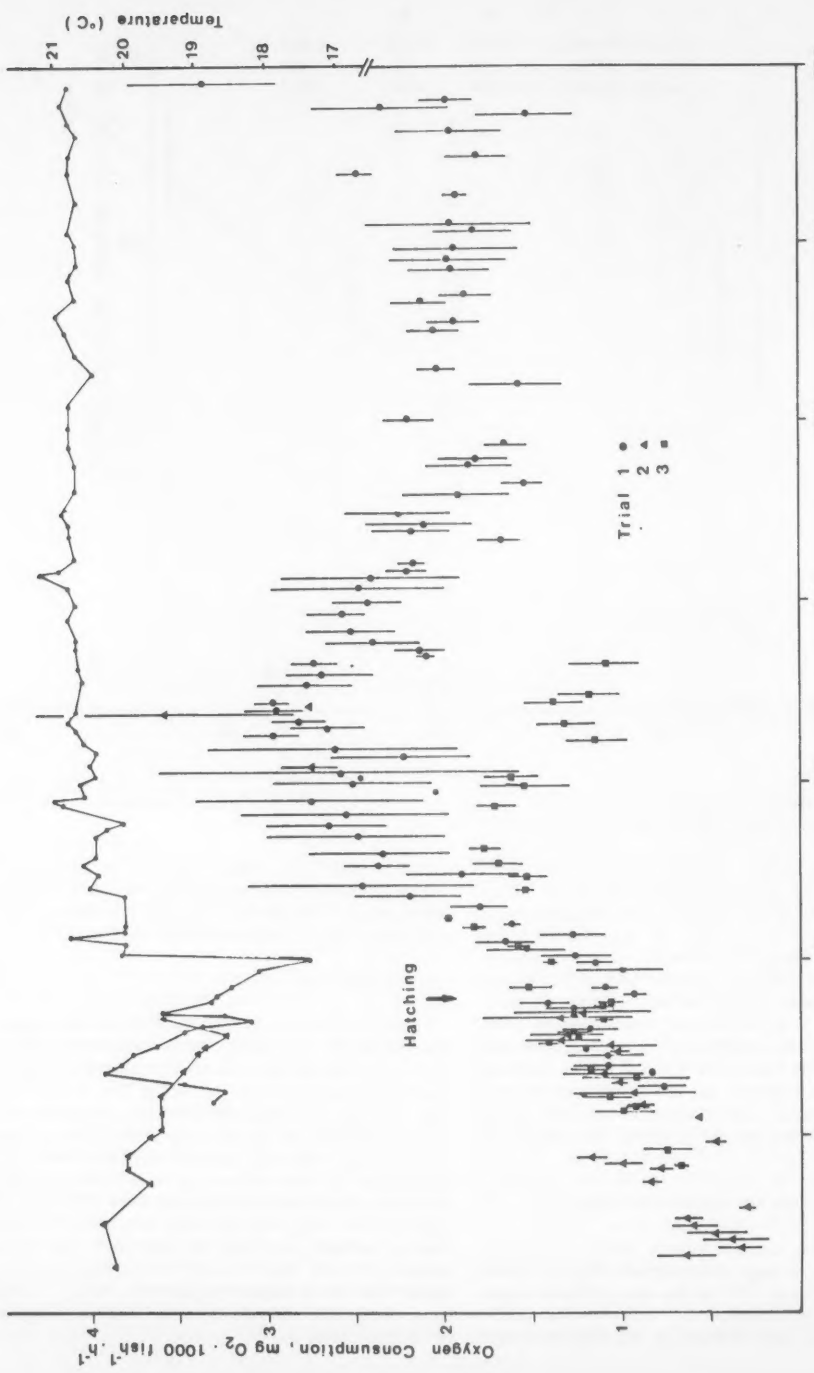

FIG. 6. Oxygen consumption rates during early ontogenesis of carp. The three trials correspond to the three batches of eggs studied. Vertical bars represent standard deviations.

TABLE 2. Cumulative data on nitrogen and energy metabolism during early development of common carp, *Cyprinus carpio*

	Stage		
	Until hatch	Prelarval and larval	Free-swimming
	Age in degree days		
	(18–80°d)	(80–170°d)	(170–350°d)
Ammonia-N excretion ($\mu g\ N \cdot ind^{-1}$)	2.348	3.190	8.331
Urea-N excretion ($\mu g\ N \cdot ind^{-1}$)	0.743	1.739	2.269
Oxygen intake ($mg \cdot ind^{-1}$),	0.072	0.203	0.437
Total energy expenditure[a] ($J \cdot ind^{-1}$)	0.965	2.720	5.855
Fat:protein ratio[b]	1.960	5.024	3.980

[a]An amount of 13.36 $J \cdot mg\ O_2^{-1}$ for ammonioteles.
[b]Ratio of fat to protein utilized in terms of energy, calculated using energy equivalents given by Elliott and Davison (1975).

Discussion

The instantaneous rate of nitrogen excretion and of oxygen consumption were consistent during the three trials made on three different batches of eggs (see Fig. 1 and 6). Urea excretion rates, measured either continuously or in 24-h collected samples were also comparable. In all the three trials, major events of ontogenesis took place at identical degree days.

During the embryonic stage, the total ammonia excretion per egg (Table 2) corresponds to 0.85% of dry weight (mean dry weight of an egg: 0.277 mg; Kamler 1976). Excretion of urea occurs all through the embryonic life, indicating synthesis even from the earliest stages of the life cycle in carp, unlike most other teleosts (Depeche et al. 1979). Excretion of urea before hatching was, however, variable. Urea has been found in the excretory products of several teleost larvae, including sea trout (Yarzhombek and Maslennikova 1971). Rice and Stokes (1974), on the other hand, did not detect any excretion of urea in rainbow trout eggs, although considerable production was noted. In the absence of information on urea cycle enzymes during ontogenesis of carp, we assume that this synthesis in carp eggs and larvae is accomplished either through arginine degradation as in rainbow trout (*Salmo gairdneri*) eggs (Rice and Stokes 1974) or through nucleotide pathways as in the adult carp (Vellas 1973). Lack of any concomitant increase in urea excretion along with that of ammonia excretion at the moment of hatching suggests that this urea production is not due to detoxification of ammonia.

The continued slow increase in oxygen consumption rates all along the embryonic development differs from the ammonia excretion pattern. Both hyperplasic and hypertrophic situations in the developing embryo exert increasing demands of oxygen from the environment. The increase in activity at the moment of hatching is not as much as in the ammonia excretion rate. The great increase in ammonia excretion during hatching is associated with the rupture of the chorionic egg membrane and with the liberation of vitelline fluids. Most of the ammonia produced during embryonic development is then massively released. This sharp increase immediately after hatching observed in carp does not occur apparently in rainbow trout (Rice and Stokes 1974) or in pink salmon (*Oncorhynchus gorbuscha*) (Bailey et al. 1980). This probably results from the more rapid development of carp and is discernible with the continuous measurement, compared to the discrete measures during a much longer developmental period of salmonids. After hatching, the small drop in oxygen consumption due to repayment of the oxygen debt incurred during cleiodic development is also of the same magnitude as that found by Kamler (1976). The stationary and subsequent increasing phases of nitrogen excretion rates between hatching and the free-swimming stage reflect the efficient utilization and the relative depletion of the endogenous yolk reserves, respectively. This latter phase also coincides with the increased mobility of the larvae.

Body protein loss of an egg until the end of endogenous feeding (estimated by Kamler (1976)) amounted to 125 μg protein (Folin-reactive). Nitrogen loss due to excretory products (ammonia plus urea) during the same period is much less (8 μg N or 50 μg N × 6.25). Both qualitative and quantitative variability has been shown in the eggs of five species of carp (Mukhopadhyay et al. 1981). Depending on the pH of extraction buffer, the protein content varied by almost 100% in *C. carpio* eggs. The physicochemical state of the proteins also changes during the course of early ontogenesis of carp (Konavalov 1979).

Great similarity exists between the pattern of oxygen consumption and that of ammonia excretion rates during the period between hatching and end of yolk absorption. When

the larvae are ready for exogenous feeding and no food is made available, they catabolize body proteins at decreasing rates until they reach the point of no return leading to massive mortality. This stage varies with different species of fish (Dabrowski 1976) and is mostly temperature-dependent. The intensive nitrogen catabolism during this phase is evidenced by the fact that nearly 57% of the total nitrogen loss since fertilization of an egg occurs during this period. The drop in oxygen consumption at the free-swimming stage is due to the transition from embryonic to gill respiration. As in the ammonia excretion pattern, initial stages of fasting slows down oxygen consumption rates as well.

The mean relative proportions of urea and ammonia excreted did not vary much between embryonic and larval stages. This is partly due to the high variability observed at all stages of development. Periodic regression analysis shows increases in successive cycles (of 24 h) both of phase angles and of daily ranges, indicative of (1) a possible internal rhythm of greater than 24 h, (2) the superposition of the metabolic processes involved in ontogenesis on the basic internal rhythm, and (3) the influence of photoperiod. Although in some cycles, it would appear preferable to employ more harmonic terms in the equation to obtain still better fits of observed data, it is reasonable to assume that a different length of internal rhythm is involved.

The combined effects of temperature and of body weight on ammonia excretion have been demonstrated in several teleosts (Guérin-Ancey 1976; Paulson 1980; Jobling 1981). In our trials, the highest temperature used (28°C) was much below the maximum tolerable limit for young stages of carp (Tatarko 1970). Even during the embryonic stage, when the optimal temperature for carp egg development is around 20°C, excretion rate continues to increase until 28°C. The relationships (Fig. 5) show that the range of temperatures we used were in the linear part of the rate–temperature curve. The higher Q_{10} observed in free-swimming larvae indicates the more thermosensitive nature of young larvae (Tatrako 1970), in comparison to younger stages.

Our results corroborate the earlier findings of Kamler (1976) regarding the intensive utilization of fats and of proteins as energy sources, and those of Lasker (1962) that the energy lost as nitrogenous excretory products is relatively small. The ratio of fat/protein utilized that would explain the oxygen consumption during a given stage of development was calculated using oxycaloric coefficients of Elliott and Davison (1975). It appears that utilization of fat as an energy source is increased during the period between hatching and free-swimming. In fasted larvae, the proportion of fats used for energy purposes remains high; 4 times more of fat than of protein, in terms of energy, is used during this early stage of exogenous feeding. Artificial diet formulations for early weaning of carp larvae should take into account the relative proportions of easily utilizable energy sources, rather than being restricted to nutritional constraints involved in protein nutrition.

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Planktonic Ciliates: Their Distribution, Abundance, and Relationship to Microbial Resources in a Monomictic Lake

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PACE, M. L. 1982. Planktonic ciliates: their distribution, abundance, and relationship to microbial resources in a monomictic lake. Can. J. Fish. Aquat. Sci. 39: 1106–1116.

The abundance, biomass, vertical distribution, and seasonal succession of planktonic ciliates were studied over a 13-mo period in a small monomictic lake. Measurements made concurrently of bacterial abundance (attached and free), chlorophyll *a*, and pheopigments were analyzed for correlations with the biomass of the major protozoan species and total protozoan biomass. Ciliate community structure varied primarily between periods of winter mixis and summer stratification. Oligotrich, tintinnid, and peritrich ciliates dominated the community during mixis (November to March). Vertical distributions tended to be uniform except for some species containing algal symbionts which occurred primarily in the photic zone. A more diverse community occurred during stratification. At this time species either tended to be restricted to the epilimnion or had sharply defined metalimnetic or hypolimnetic maxima. With the development of anoxia in the hypolimnion (June), bacterivorous scuticociliates reached high densities in the metalimnion and upper hypolimnion and dominated the community in terms of density and to a lesser extent biomass. Total protozoan (ciliates and the amoeba *Difflugia*) density varied over the annual cycle between 1 and $50 \times 10^7 \cdot m^{-2}$ (0.1 to $189 \times 10^3 \cdot L^{-1}$) while biomass as measured by volume varied between 6 and 60 $mm^3 \cdot m^{-2}$ (61–610 mg dry wt $\cdot m^{-2}$ and 1.57–1260 $\mu m^3 \cdot L^{-1}$). Highest densities occurred from August through October when scuticociliates were abundant, but peak biomass occurred in November with a bloom of the large peritrich *Rhabdostyla* sp. Total ciliate biomass was correlated only with the concentration of pheopigments, but when the biomass due to *Rhabdostyla* was subtracted from the total, significant correlations were observed between protozoan biomass and chlorophyll *a*, pheopigments, attached bacteria, and free bacteria. Correlations between the biomass of specific ciliates and microbial parameters, as well as observations of their vertical and seasonal distributions, suggest that concentrations of appropriate food resources are important in determining the abundance of heterotrophic ciliates in the plankton.

Key words: ciliates, plankton, protozoa, amoebae, lakes, monomictic, zooplankton, chlorophyll *a*, pheopigments, bacteria

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Nous avons suivi durant 13 mois l'abondance, la biomasse, la distribution verticale et la succession saisonnière des ciliés planctoniques dans un petit lac monomictique. Des mesures simultanées d'abondance des bactéries (fixées et libres), de la chlorophylle *a* et des phéopigments ont été analysées en vue de détecter des corrélations entre ces dernières et la biomasse des principales espèces de protozoaires et la biomasse totale des protozoaires. La structure de la communauté de ciliés varie surtout dans l'intervalle qui sépare le mélange hivernal et la stratification estivale. Au moment du mélange (novembre à mars), les oligotriches, tintinnoïdes et péritriches prédominent. Sauf pour certaines espèces contenant des symbiontes algaux et se trouvant surtout dans la zone photique, la distribution verticale des ciliés tend à être uniforme. En période de stratification, on observe une communauté plus diversifiée. À cette époque, les espèces tendent a être restreintes à l'épilimnion, ou exhibent des maxima métalimnétiques ou hypolimnétiques bien définis. À l'époque de formation de

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l'anoxie dans l'hypolimnion (juin), les scuticociliés se font très denses dans le métalimnion et l'hypolimnion supérieur et, en termes de densité et, à un degré moindre, de biomasse existante, dominent la communauté. La densité totale des protozoaires (ciliés et l'amibe *Difflugia*) varie cycliquement de 1 à 50 × $10^7 \cdot m^{-2}$ (0,1 à 189 × 10^3 L^{-1}). La biomasse, d'autre part, mesurée en volume, varie de 6 à 60 mm^3 m^{-2} (61 à 610 mg de poids sec m^{-2} et 1,57 à 1 260 μm^3 L^{-1}). Les densités maximales se rencontrent entre août et octobre, période d'abondance des scuticociliés. Par ailleurs, le maximum de biomasse se produit en novembre, au moment d'une floraison du péritriche de grande taille *Rhabdostyla*. La biomasse totale des ciliés ne montre une corrélation qu'avec la concentration des phéopigments. Si toutefois l'on soustrait du total la biomasse produite par *Rhabdostyla*, on trouve des corrélations significatives entre la biomasse des protozoaires et la chlorophylle *a*, les phéopigments, les bactéries fixées et les bactéries libres. Ces corrélations entre la biomasse de ciliés particuliers et les paramètres microbiens, ainsi que leur distribution verticale et saisonnière donnent à penser que, dans la détermination de l'abondance des ciliés hétérotrophes dans le plancton, les concentrations de ressources alimentaires appropriées jouent un rôle important.

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NAUWERCK (1963) in his classical study of the Lake Erken plankton commented that planktonic ciliates are rarely included in limnological investigations. This remains true despite his and several other studies (Korniyenko 1972; Sorokin and Paveljeva 1972; Rigler et al. 1974; Bownik-Dylinska 1975; Mamaeba 1976; Petrova et al. 1976; Hecky and Kling 1981) which show that the ciliated Protozoa are at least periodically important components of the plankton. These organisms are difficult to observe and quantify. They are not effectively sampled by nets, nor do they preserve well in formaldehyde solutions (Pace and Orcutt 1981). The conception, however, that ciliates are unimportant in the economy of freshwater pelagic ecosystems is probably more important in explaining why they have been neglected. Hutchinson (1967) noted their potential importance by "analogy with the oceanic plankton" but suggested that rotifers have filled the niche of ciliates in the freshwater plankton. More recent reviews and symposia in zooplankton ecology either make no mention of ciliates (Hall et al. 1976; Porter 1977; Kerfoot 1980) or categorically deny their significance (Hrbáček 1977).

With these conceptual and technical difficulties it is not surprising that little is known about the distribution and abundance of ciliates both within and between lakes. Previous quantitative studies indicate that densities range from 10^2 to 10^4 ciliates$\cdot L^{-1}$ in oligotrophic and mesotrophic lakes (Nauwerck 1963; Rigler et al. 1974; Petrova et al. 1976), while densities up to $10^5 \cdot L^{-1}$ have been observed in some eutrophic lakes (Korniyenko 1972; Sorokin and Paveljeva 1972) and ponds (Wilbert 1969). Ciliate biomass at times accounts for a large component of the zooplankton biomass (Nauwerck 1963; Korniyenko 1972; Sorokin and Paveljeva 1972; Mamaeba 1976); in Lake Tanganyika at some sites it actually exceeds algal standing crops (Hecky and Kling 1981). Few of these studies, however, provide data on how the abundance of individual taxa changes with depth or describe in any detail the seasonal succession of the ciliate community.

The purpose of this study is to describe quantitatively an assemblage of planktonic ciliates over the annual cycle of a lake. The relative importance of planktonic protozoans within a zooplankton community is reported elsewhere (Pace and Orcutt 1981). Here, data on the distribution, abundance, biomass, and seasonal succession of the major taxa within the ciliate community are presented. Correlations between ciliate biomass and the abundance of their algal and bacterial resources are also presented, and general hypotheses to explain ciliate community structure are proposed.

Methods

Planktonic ciliates were sampled at monthly intervals from December 1978 to December 1979 in Lake Oglethorpe, a small monomictic lake (30 ha, z_{max} = 8.5 m, $\bar{z}$ = 3 m) located 20 km southeast of Athens, Georgia. Lake Oglethorpe is eutrophic in terms of nutrient chemistry (range of total phosphorus = 16−1078 $\mu g \cdot L^{-1}$) and bacterial densities (range of total counts = 1.5−32 × 10^6 cells$\cdot mL^{-1}$), but primary production rates are moderate, 100−200 g $C \cdot m^{-2} \cdot yr^{-1}$ (J. Meyer and T. Jacobsen, University of Georgia, Athens, GA, unpublished data). The modest productivity is attributed to seasonally high levels of turbidity (Secchi depths as low as 0.5 m) caused by suspended clays from watershed runoff and vertical mixing. Protozoan samples were taken at 1-m intervals from surface to bottom with a 5-L Van Dorn bottle at a deep central station (z = 8 m). A 230-mL subsample from the water bottle was preserved with 10 mL of a saturated solution of $HgCl_2$, and stained with a drop of 0.04% bromophenol blue (M.B. Csutor, Danube Research Station, Budapest, Hungary, personal communication). Another portion (0.5−2.0 L) of the water bottle sample was gently filtered through a 26-μm sieve to sample larger colonial and testate forms. The sieve was thoroughly rinsed, and the contents preserved in $HgCl_2$. Although rigid forms were effectively sampled by sieving, naked ciliates as large as *Paradileptus* (48 × 191 μm) were observed in the filtrate after sieve passage and thus could not be quantified from sieved samples. Mercuric chloride was an effective preservative for Protozoa (Pace and Orcutt 1981), and the bromophenol blue stain aided

TABLE 1. The major protozoan taxa of Lake Oglethorpe, their maximum width and length, and estimated volume.

Taxon		Size (μm)	Volume ($\mu m^3 \times 10^3$)
Phylum Ciliophora			
Order Primociliatida			
Loxodes sp.		64×154	329.0
Order Prostomatida			
Gymnostomes[a]		43×53	51.5
Coleps sp.		31×42	21.1
Urotricha sp.		26×31	11.5
Order Haptorida			
Askenesia volvox		32×32	17.6
Mesodinium sp.		15×28	1.6
Paradileptus sp.		48×191	135.1
Spathidium sp.		46×91	79.8
Order Pleurostomatida			
Litonotus sp.		23×107	21.2
Order Hymenostomatida			
Lembadion magnum		50×100	65.9
Stokesia vernalis		43×46	47.2
Order Scuticociliatida			
Scuticociliates[b]		15×30	3.6
Order Peritrichida			
Epistylis rotans		38×58	409.3[c]
Rhabdostyla sp.		109×123	759.8
Vorticella sp. 1		45×47	50.9[c]
Vorticella sp. 2		22×23	6.0
Order Heterotrichida			
Condylostoma sp.		69×82	205.8
Order Oligotrichida[d]			
Small (<30 μm)[e]	M	24×25	7.7
	S	22×23	6.1
Large (>40 μm)[f]	M	43×45	43.1
	S	44×44	44.6
Srombidium viride	M	33×44	12.0
	S	32×37	9.8
Tintinnopsis lacustris		44×63	70.6
Phylum Sarcomastigophora			
Difflugia sp.		63×71	150.0

[a]Several species of the genera *Prorodon* and *Holophyra*.
[b]Several species of the genera *Uronema* and *Dexiotricha*.
[c]For the Peritrichida, *E. rotans* and *Vorticella* sp. 1, dimensions of an average cell are shown, but volumes are for an average colony or aggregation.
[d]For the Oligotrichida present in the plankton throughout the year, average dimensions and volumes are listed for mixis (M) and stratified (S) periods.
[e]Several species of the genera *Strombidium* and *Halteria*.
[f]Several species of the genus *Strombilidium*.

in observing these protozoans particularly when detritus and clays were abundant in the water column.

Ciliates were allowed to settle for at least 12 h in plankton chambers and were counted with an inverted microscope. For whole water samples, volumes of 5, 10, or 25 mL (depending on ciliate density and the concentration of other particulates) were counted at 250× magnification. Because of the time required to count samples (2−5 h per sample), variability due to spatial heterogeneity and sampling error was not considered in this study. Replicate subsample counts (10-mL volume) of the whole water samples were in agreement with a Poisson series ($\chi^2 = 1.674$, $P < 0.5$). Confidence limits for a single count can thus be estimated by assuming that the variance equals the mean (Elliot 1977). Total counts generally exceeded 100 individuals for each sample; therefore, 95% confidence limits for single counts were ±20% or less. The filtered samples were poured into several settling chambers, and the whole sample counted at 100× magnification.

Most ciliates were identified to genus and in some cases to species by consulting the general works of Fauré-Fremeit (1924), Kahl (1930−1935), Noland (1959), Dingfelder (1962), Bick (1972a, b), Corliss (1979), and more specific studies of particular groups and genera by Weinrich (1929a, b), Noland and Finley (1931), Noland (1937), Jankowski (1964), Dragesco (1966), Tamar (1965, 1973), Fauré-Fremeit (1968), and Taylor et al. (1971). A testate amoeba was also found in the plankton and identified using Grospeitch (1972).

To determine biomass, volumes of the individual taxa were

estimated by assuming cells approximated simple, or combinations of simple, geometric shapes. This procedure was not wholly satisfactory, partly because ciliate shapes do not always conform well to simple geometric shapes. Preservation may also alter the shape of these protozoans. While most ciliates retained their form with little shrinkage in mercuric chloride, for some species the natural shape was altered on contact with the preservative. In addition to problems of preservation and approximation of shape, volume-to-biomass ratios may not always be constant, varying both within and between species as demonstrated for rotifers by Latja and Salonen (1978). Despite these limitations, volume estimates do give a relative idea of the biomass of various taxa and the gross dynamics of the ciliate fauna.

For the taxa present throughout the year, appropriate measurements to estimate volume were made on 10 individuals from four different sampling times (total = 40) including both stratified and unstratified periods (Table 1). Ten individuals from two different sampling times (total = 20) were measured in taxa which were seasonally abundant. Measurements were made to the nearest 1.2 μm at 1000× (3.1 μm at 400× for *Paradileptus* sp. only) using an ocular micrometer. Observations of cells fixed by $HgCl_2$, although useful for distinguishing gross morphological features, did not provide the cytological detail necessary for precise identification. Thus, in some cases closely related species were "lumped" together into operationally defined taxonomic units (Table 1). The classification of taxa is based on Corliss (1979).

Concurrently with the collection of protozoans, samples were also gathered from the same 5-L Van Dorn bottles for their microbial resources. Phytoplankton pigments, a measure of algal biomass, were determined by a high-pressure liquid-chromatographic method (Jacobsen 1978) and bacterial densities by direct counts using epifluorescence microscopy with acridine orange as a stain (Porter and Feig 1980). Correlation coefficients were calculated for chlorophyll *a*, pheopigments, attached bacteria (bacteria attached to organic and inorganic particles), free bacteria (bacteria not attached to particles), and the biomass of the major protozoan taxa on a volumetric basis. Correlations were also calculated between the microbial parameters and total protozoan biomass on an areal basis. In each case, the null hypothesis of no association between the variables was tested. All data were $\log_{10}$ transformed because variances tended to be greater than the mean. This transformation effectively normalized the areal data as determined by a Kolmogorov Smirnov test. For the volumetric data, 25% of the variables were not normalized by the log transformation. Consequently, Spearman rank correlations (nonparametric) were determined for the volumetric data, and Pearson correlations (parametric) were calculated for the areal data.

Results

The annual cycle of a monomictic lake can be partitioned into mictic and stratified periods. In Lake Oglethorpe, mixis occurs from November to March and stratification from April to October. At the onset of stratification, oxygen begins to be depleted in the hypolimnion, and these waters are anaerobic from May until fall overturn (Pace 1981). Transitions between mixis and stratification occur over a period of weeks with temperature stratification beginning in March and a gradual erosion of the thermocline beginning in late September. The conditions which prevailed during mixis, stratification, and the transitions between them have a major effect on the abundance, biomass, and distribution of ciliates and on the structure of the ciliate community.

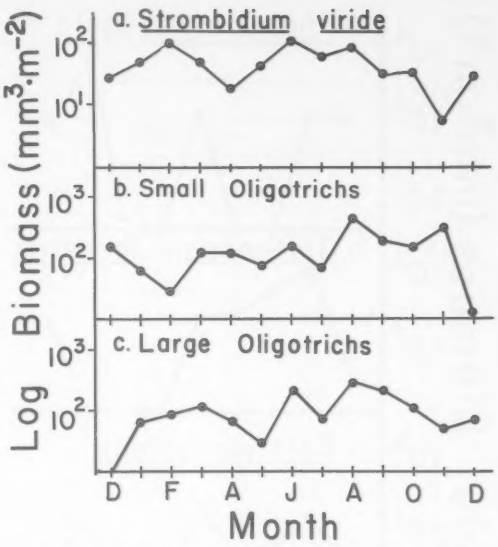

FIG. 1. Biomass of the major ciliate taxa found throughout the year, (a) *Strombidium viride*, (b) Small oligotrichs, (c) Large oligotrichs.

WINTER MIXIS

During winter mixis, the oligotrichs (*Strombidium viride* and the operationally defined small and large oligotrich taxa, see Table 1) and a distinct winter fauna were present in the plankton. Oligotrichs were found throughout the year and were always a significant component of the protozoan community. Maximum volumes for these taxa during mixis ranged from 100 to 300 $mm^3 \cdot m^{-2}$ (Fig. 1). The dominant ciliates of the winter fauna were the peritrichs, *Epistylis rotans* (maximum volume = 180 $mm^3 \cdot m^{-2}$) and *Rhabdostyla* sp. (maximum volume = 5600 $mm^3 \cdot m^{-2}$), and the tintinnid, *Tintinnopsis lacustris* (maximum volume = 960 $mm^3 \cdot m^{-2}$). These species appeared in the plankton after fall overturn, and all three declined to low densities after April (Fig. 2).

Vertical distributions of ciliates during mixis tended to be uniform with the exception of *S. viride* which was always more abundant in the upper half of the water column (Pace 1981; Pace and Orcutt 1981). This species contains symbiotic zoochlorellae (Fauré-Fremeit 1924; Bick 1972a), and its pattern of distribution suggests a partial dependence on autotrophy for nutrition.

In all months except January the small oligotrichs or *S. viride* were numerically the most important ciliates (Table 2). *Rhabdostyla* sp. dominated community biomass in

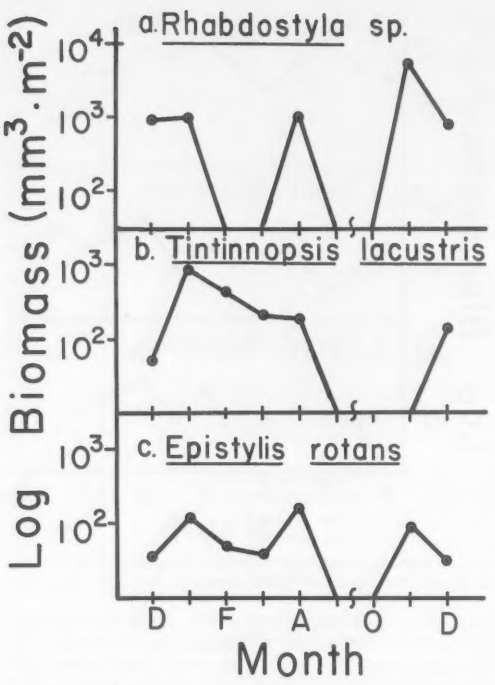

FIG. 2. Biomass of the major ciliates found during mixis (a) *Rhabdostyla* sp., (b) *Tintinnopsis lacustris*, (c) *Epistylis rotans*. Note that the monthly scale is broken with the months of June through September excluded.

all months except February and March when it occurred at very low densities. *Tintinnopsis lacustris* was an important species from January through March both in terms of density and biomass.

STRATIFICATION

A more diverse protozoan community occurred during stratification than during mixis with up to 12 taxa of ciliates and one genus of amoeba contributing at least 5% to the total density or biomass (Table 3). Within a given month, however, the percentage density or biomass was typically skewed towards one or a few groups.

There were two general patterns of vertical distribution during stratification. Species were either restricted to the aerobic epilimnion or had sharply defined metalimnetic or hypolimnetic maxima (Pace 1981; Pace and Orcutt 1981). A gradual change occurred during stratification with biomass dominance shifting from winter and epilimnetic forms to summer meta- and hypo-limnetic ciliates. April was a transition month with the mixis forms *Rhabdostyla* sp. and *E. rotans* dominating (Table 3). In May the epilimnetic amoeba, *Difflugia* sp., reached a peak biomass of 395 $mm^3 \cdot m^{-2}$ (Fig. 3a) and accounted for 61% of the total community biomass (Table 3). Taxa occurring primarily in the meta- and hypo-limnion such as the gymnostomes (Fig. 3b) and the scuticociliates (Fig. 3c) began to dominate the community in June (Table 3). These ciliates and others with similar distributions (*Lembadion magnum* and *Coleps* sp.) were found at high biomasses throughout the summer and fall with maximum biomasses of gymnostomes (880 $mm^3 \cdot m^{-2}$) and scuticociliates (1200 $mm^3 \cdot m^{-2}$) occurring in October just prior to fall overturn (Fig. 3).

TOTAL ABUNDANCE AND BIOMASS OF PROTOZOA

Protozoan (here used to refer to ciliates and the amoeba *Difflugia*) abundance fluctuated little during winter mixis and spring varying between 2 and 5 $\times$ $10^7 \cdot m^{-2}$ (Fig. 4). In June there was a marked increase in abundance with high concentrations ($>10^8 \cdot m^{-2}$) maintained through October. This increase was due to the development of a meta- and hypolimnetic fauna as well as an increase in both the diversity and density of the epilimnetic fauna. After October, protozoan density declined to winter levels.

Seasonal variations in total biomass as estimated by volume ($mm^3 \cdot m^{-2}$) were more irregular (Fig. 4), reflecting not only changes in density but shifts in the size structure of the protozoan community. Biomass maxima in January and April were due to *Rhabdostyla* and *Tintinnopsis* in the first case and *Rhabdostyla* and *Epistylis* in the second. Biomass was higher in the summer and fall except for a decline in July. This decline was due primarily to a decrease in the density of some of the larger ciliates (the gymnostomes and *Stokesia*). Highest protozoan biomass was observed in November when the overall density of protozoans declined sharply (Fig. 4). This biomass peak was due to a bloom of the peritrich, *Rhabdostyla*.

CORRELATIONS WITH MICROBIAL RESOURCES

Means and ranges of the microbial parameters used in the correlation analysis are presented in Table 4. A detailed discussion of the bacterial counts can be found in Porter and Feig (1980), and information on the interaction of both autotrophic and heterotrophic standing stocks and processes is forthcoming (K. G. Porter, University of Georgia, Athens, GA, personal communication). In general during mixis, mean values of the microbial parameters were 2–3 times less than the means for stratification. Both pigment concentrations and bacterial densities tended to be uniform with depth during mixis, except for occasional high concentrations of chlorophyll (2–4 $\mu g \cdot L^{-1}$) between 0 and 1 m. Maximum concentrations of chlorophyll (3.4–29.5 $\mu g \cdot L^{-1}$) during stratification generally occurred at the top of the thermocline with pheopigment maxima sometimes corresponding to chlorophyll maxima and sometimes occurring elsewhere in the water column. Free bacteria were always an order of magnitude more abundant than attached forms (Table 4), and both types of bacteria were most abundant in the upper hypolimnion from June through August.

Positive and significant ($P < 0.05$) correlations for these parameters and the major taxa of protozoa (Table 5) are interpreted here as indicative of the resources most important to a protozoan taxa. These inferences, however, are tentative

TABLE 2. Community structure during mixis in terms of the percentage contribution of the major ciliate taxa to (a) total density and (b) biomass. Ciliates included accounted for at least 5% of the density or biomass during any 1 mo.

Taxon	1978	1979				
	Dec.	Jan.	Feb.	March	Nov.	Dec.
a) Density						
Strombidium viride	8.7	13.7	39.8	15.9	0.9	51.1
Small oligotrichs	80.9	28.8	16.8	59.6	78.0	11.0
Large oligotrichs	0.0	4.7	9.1	10.4	2.0	11.2
Tintinnopsis lacustris	2.7	47.2	31.6	12.0	0.0	13.8
Epistylis rotans	0.4	1.1	0.6	0.4	0.5	0.6
Rhabdostyla sp.	4.8	4.5	0.0	0.0	13.8	7.7
Other	2.5	0.0	2.1	1.8	4.8	4.6
b) Biomass						
Strombidium viride	2.2	2.1	13.4	8.6	0.1	7.9
Small oligotrichs	13.2	2.8	3.5	20.2	5.2	1.0
Large oligotrichs	0.0	2.7	11.0	20.2	0.8	5.9
Tintinnopsis lacustris	4.1	42.7	61.1	37.3	0.0	11.5
Epistylis rotans	3.1	5.5	6.4	6.7	1.7	2.8
Rhabdostyla sp.	77.2	44.1	0.0	0.6	91.3	69.7
Other	0.2	0.0	4.6	6.3	0.9	1.3

TABLE 3. Community structure during stratification in terms of the percentage contribution of the major ciliate taxa and the amoeba *Difflugia* to (a) total density and (b) biomass. Protozoans included accounted for at least 5% of the density or biomass during any 1 mo.

Taxon	Apr.	May	June	July	Aug.	Sept.	Oct.
a) Density							
Strombidium viride	4.2	16.9	9.4	4.1	2.1	1.0	0.9
Small oligotrichs	50.5	48.4	19.7	7.3	15.5	11.5	5.8
Large oligotrichs	3.6	2.4	4.2	1.0	1.6	1.6	0.6
Rhabdostyla sp.	3.5	0.0	0.0	0.0	0.0	0.0	0.0
Difflugia sp.	1.3	9.7	0.7	0.4	0.3	0.1	0.0
Scuticocialiates	26.3	4.7	21.6	80.4	72.4	58.0	83.6
Mesodinium sp.	0.0	6.9	6.7	1.0	1.5	8.1	2.4
Paradileptus sp.	0.0	0.0	0.4	0.3	0.0	0.5	0.0
Condylostoma sp.	0.0	0.0	0.6	0.1	1.0	0.0	0.0
Lembadion magnum	0.0	0.0	1.4	1.1	0.9	0.4	0.0
Gymnostomes	0.0	0.0	11.2	2.6	1.7	1.5	4.1
Stokesia vernalis	0.0	0.0	19.3	1.2	1.1	9.1	0.0
Coleps sp.	0.0	0.0	0.0	0.0	0.0	5.3	1.0
Other	10.5[a]	10.9	4.7	0.6	2.1	2.8	1.8
b) Biomass							
Strombidium viride	0.9	7.0	3.8	4.9	2.2	0.9	1.3
Small oligotrichs	6.7	12.5	4.9	5.4	10.2	6.0	6.1
Large oligotrichs	3.5	4.5	7.5	5.5	7.4	6.1	4.0
Rhabdostyla sp.	57.2	0.0	0.1	0.0	0.0	0.0	0.1
Difflugia sp.	4.1	61.0	4.3	6.4	5.2	1.6	0.9
Scuticociliates	2.0	0.7	3.2	35.0	28.0	17.7	46.0
Mesodinium sp.	0.0	0.5	0.4	0.2	0.3	1.1	0.6
Paradileptus sp.	0.0	0.0	2.4	4.5	0.3	6.2	0.5
Condylostoma sp.	0.0	0.0	5.0	3.4	22.5	0.0	0.0
Lembadion magnum	0.0	0.0	3.7	9.0	6.2	2.5	0.2
Gymnostomes	0.0	0.0	23.6	16.3	9.2	6.6	32.6
Stokesia vernalis	0.0	0.0	37.2	6.6	5.5	36.6	0.1
Coleps sp.	0.0	0.0	0.0	0.0	0.0	9.5	3.4
Other	25.7[a]	13.9	4.0	2.9	3.1	5.2	4.2

[a]Includes the mixis forms *Tintinnopsis lacustris* and *Epistylis rotans* which during stratification only occurred in April.

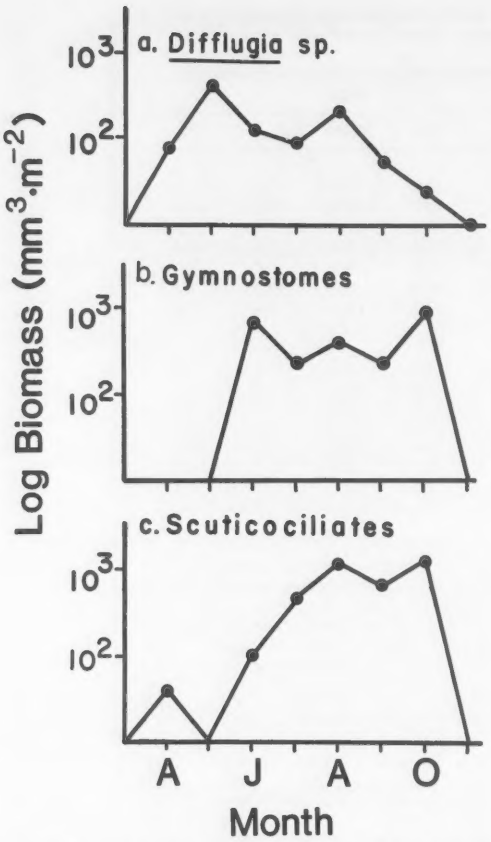

FIG. 3. Biomass of some of the major protozoans found during stratification (April 1979 through October 1979) (a) *Difflugia* sp., (b) Gymnostomes, (c) Scuticociliates.

because resources may covary with some other parameter important in determining the biomass of a protozoan (e.g. temperature, oxygen concentration, predator density), and thus the correlations could be misleading. In addition, lack of significant correlations should also be interpreted cautiously, because a protozoan may, for example, feed on only a few algae and thus not correlate well with a parameter measuring the total algal biomass (i.e. chlorophyll).

For the ciliates present only during mixis, no significant correlations were observed (Table 5). The correlation coefficients, however, between biomass and chlorophyll *a* for *E. rotans* and *T. lacustris* approached the 0.05 significance level ($P = 0.08$ and 0.09, respectively). The biomass of *Rhabdostyla* sp. was not significantly correlated with any of the four microbial parameters, but living specimens of *Rhabdostyla* were observed with food vacuoles packed with clay particles. Perhaps, these clay particles which were particularly abundant during mixis contained sufficient adsorbed

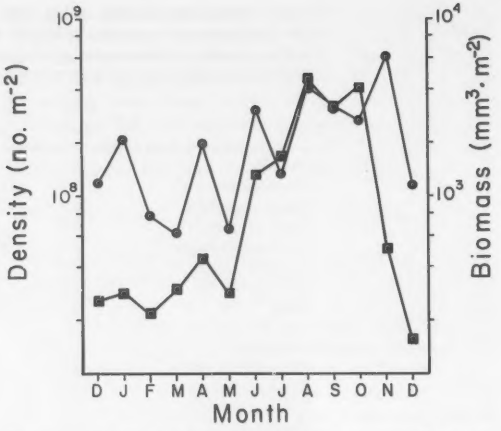

FIG. 4. Annual cycle of abundance (■) and biomass (●) for the planktonic protozoans of Lake Oglethorpe.

organic matter and attached bacteria ($r = 0.25$, $P = 0.09$) to support the growth of this ciliate.

Both the small and large oligotrichs had significant correlations with pheopigments and attached bacteria or free bacteria. The implication is that these taxa may be feeding on dead or dying algae and the bacteria associated with algal decomposition. The biomass of both *S. viride* and *Difflugia* sp. was not significantly correlated with any of the microbial parameters despite a large number of observations for both species (Table 5). These protozoa contain algal symbionts and thus fluctuations in their biomass may be partially independent of resources.

For many of the ciliates present during stratification, the number of observations was limited and in several cases (*Mesodinium*, *Vorticella*, *Paradileptus*, *Stokesia*) no significant patterns were observed. Three taxa *L. magnum*, *Coleps* sp., and the gymnostomes, which were most abundant in the metalimnion, were correlated with chlorophyll *a* which was maximal in the lower epilimnion and metalimnion during stratification.

Highly significant positive correlations were observed between scuticociliate biomass and all of the microbial parameters. These relationships indicate that the scuticociliates occur in zones of high algal and bacterial biomass. In the lake, scuticociliate maxima were found at the thermocline, a depth of high pigment concentrations and high bacterial densities.

Positive relationships were found in all cases between the microbial parameters and total protozoan biomass $\cdot m^{-2}$ (Table 6), but only the concentration of pheopigments was significantly related to total biomass. Total biomass, however, was strongly influenced by *Rhabdostyla*, a species which dominated the community when present (Tables 2 and 3) and was not closely related to any of the microbial parameters (Table 5). When the biomass due to *Rhabdostyla* was subtracted from the total, significant correlations were observed between protozoan biomass and chlorophyll *a* ($P = 0.015$), pheopigments ($P = 0.014$), attached bacteria ($P = 0.021$), and free bacteria ($P = 0.004$).

TABLE 4. Means and ranges of microbial parameters on both a (a) volumetric and (b) areal basis for mixis (November through March) and stratified periods (April through October) in Lake Oglethorpe. Pigment concentrations are in terms of $\mu g \cdot L^{-1}$ and $mg \cdot m^{-2}$ while bacterial counts are in terms of no. $\times 10^5$ mL^{-1} and no. $\times 10^6$ cm^{-2} on a volumetric and areal basis, respectively.

	Mixis		Stratified	
	Mean	Range	Mean	Range
a) Volumetric				
Chlorophyll *a*	1.6	0.3–4.3	4.0	0.3–29.5
Pheopigments	0.9	0.3–1.9	1.9	0.1–9.5
Attached bacteria	3.0	0.6–46.5	9.8	0.3–46.5
Free bacteria	45.5	14.6–76.4	139.8	52.8–301.3
b) Areal				
Chlorophyll *a*	10.4	3.3–16.8	25.4	8.1–72.7
Pheopigments	6.5	3.3–16.1	12.9	8.3–29.2
Attached bacteria	2.1	1.5–4.2	5.0	1.1–19.1
Free bacteria	32.7	17.9–45.8	98.0	54.1–174.4

TABLE 5. Spearman correlation coefficients between the major protozoan taxa (μm^3 L^{-1}) and the microbial parameters. Significant correlations are noted by $*P < 0.05$, $**P < 0.01$, $***P < 0.005$.

Taxa	n[b]	Chlorophyll *a*, $\mu g \cdot L^{-1}$	Pheopigments, $\mu g \cdot L^{-1}$	Attached bacteria, no. mL^{-1}	Free bacteria, no. mL^{-1}
Rhabdostyla sp.	44[a]	0.207	0.106	0.252	0.090
Epistylis rotans	53[a]	0.245	0.230	−0.167	0.068
Tintinnopsis lacustris	45	0.259	−0.009	−0.188	−0.185
Strombidium viride	84[a]	0.127	−0.013	−0.050	0.129
Small oligotrichs	98[a]	−0.027	0.244*	0.353***	0.181
Large oligotrichs	71[a]	0.064	0.322**	0.276*	0.395***
Scuticociliates	52[a]	0.551***	0.514***	0.526***	0.750***
Difflugia sp.	59[a]	−0.139	−0.071	−0.066	0.005
Mesodinium sp.	36	−0.185	0.099	−0.143	−0.098
Vorticella sp.	28	−0.373	0.264	−0.029	0.247
Paradileptus sp.	12	0.293	−0.032	0.088	0.382
Lembadion magnum	19	0.652*	0.429	0.054	0.137
Condylostoma sp.	13	−0.313	0.340	−0.542	0.050
Gymnostomes	31	0.421*	0.147	−0.187	0.177
Stokesia vernalis	23	−0.068	0.123	−0.122	0.227
Coleps sp.	8	0.905***	0.690	0.809*	0.690

[a] n for bacterial counts (attached and free) equals $n + 1$.
[b] n = number of observations.

TABLE 6. Pearson correlation coefficients between protozoan biomass ($mm^3 \cdot m^{-2}$), protozoan biomass less that due to *Rhabdostyla* sp., and the microbial parameters. All data were $\log_{10}$ transformed monthly values ($n = 13$). Significant correlations are noted by $*P < 0.05$, $**P < 0.01$.

	Chlorophyll, $mg \cdot m^{-2}$	Pheopigments, $mg \cdot m^{-2}$	Attached bacteria, no. cm^{-2}	Free bacteria, no. cm^{-2}
Protozoan biomass	0.283	0.558*	0.525	0.428
Protozoan biomass − *Rhabdostyla* sp.	0.657*	0.663*	0.630*	0.733**

Discussion

At all sampling times in this study, planktonic ciliates were abundant. Over the annual cycle, densities varied between 1 and 50 $\times 10^7 \cdot m^{-2}$ and 10^2 to $10^5 \cdot L^{-1}$. The limited available data summarized in Table 7 indicate that the concentrations of ciliated Protozoa found in Lake Oglethorpe are not unusual. In oligotrophic lakes annual mean densities of ciliates range from 2 to 11 $\times 10^3 \cdot L^{-1}$, in mesotrophic lakes from 18 to 71 $\times 10^3 \cdot L^{-1}$, and in eutrophic lakes from 56 to 156 $\times 10^3$ L^{-1}. There is a trend for ciliates to increase in abundance with increasing productivity among lakes (Table 7). Beaver and Crisman (1982) have found a

TABLE 7. Summary of data on densities and biomass of planktonic ciliates in lakes.

Lake	Range of observed densities ($\times 10^3 \cdot L^{-1}$)	Annual range of biomass	Annual mean density ($\times 10^3 \cdot L^{-1}$)	Trophy	References
Char	0–10.3	2.1–15.6 mg dry wt m^{-2}	2.4	Ultraoligotrophic	Rigler et al. (1974)
Floridian lakes (4)			10.8	Oligotrophic	Beaver and Crisman (1982)
Russian lakes (2)	0.5–6.3		2.3	Oligotrophic	Petrova et al. (1976)[a]
Tanganyika		10–460 mg wet wt m^{-3}		Oligotrophic	Heckey and Kling (1981)
Erken	0.1–10			Mesotrophic	Nauwerck (1963)
Oktyabr'skoye	2–254		70.9	Mesotrophic	Korniyenko (1972)
Floridian lakes (8)			25.1	Mesotrophic	Beaver and Crisman (1982)
Oglethorpe	0.1–190	61–610 mg dry wt m^{-2}[b]	18.0	Meso–eutrophic	This study[c]
Mikalajskie	0.5–8.0	25–270 mg wet wt m^{-3}		Eutrophic	Bownik-Dylinska (1975)[c]
Floridian lakes (2)			55.5	Eutrophic	Beaver and Crisman (1982)
Dalnee	0–230			Eutrophic	Sorokin and Paveljeva 1972)[a]
Karasum	14–808		145.1	Eutrophic	Korniyenko (1972)
Floridian lakes (4)			155.5	Hypereutrophic	Beaver and Crisman (1982)

[a]Samples in these studies taken only during the productive period of the annual cycle.
[b]Dry weights estimated from volume assuming a specific gravity of 1.0 and a dry weight to wet weight ratio of 10%.
[c]Ciliates and the amoeba *Difflugia* sp.

highly significant positive relationship (regression, $r^2 = 0.91$) between "trophic state index" (based on chlorophyll concentrations) and mean annual ciliate density in 20 Floridian lakes. The mean annual density of protozoans (ciliates plus the amoeba *Difflugia*) found in Lake Oglethorpe was $18.0 \times 10^3 \cdot L^{-1}$. This is at the low end of the range observed by Beaver and Crisman (1982) for mesotrophic lakes in Florida, and in general, ciliate densities found in subtropical Floridian lakes appear to be higher than those observed for temperate lakes covering a range of trophies (Nauwerck 1963; Sorokin and Paveljeva 1972; Bownik-Dylinska 1975; Petrova et al. 1976). While temperate lakes may have lower densities than subtropical systems, the single arctic lake studied has a higher density of ciliates (Table 7) than expected considering the extreme oligotrophy of Char Lake (Rigler et al. 1974). Substantially more quantitative data on planktonic protozoans are required before any of these apparent latitudinal differences can be confirmed.

Most planktonic ciliates have a wide tolerance to temperature and various physical and chemical conditions (Bick 1972a, b). Ciliates, however, require high concentrations of food to sustain population growth (Fenchel 1980). Three general patterns of feeding can be hypothesized for planktonic ciliates, and it is these patterns that probably determine the seasonal succession of the assemblage in Lake Oglethorpe.

First, some species may be specialized in their resource requirements. Two of the ciliates present during mixis in Lake Oglethorpe appear to be specialists. At this time, the algal community is dominated by small flagellates, cryptomonads, and diatoms (K. Porter, unpublished data). In addition, there are high concentrations of fine clay particles from watershed runoff in the plankton. *Tintinnopsis lacustris* probably feeds principally on the small algal flagellates like other tintinnids (Heinbokel 1978; Stoecker et al. 1981). Observations of *Rhabdostyla* sp. indicate that this protozoan ingests clay particles perhaps utilizing the attached bacteria. As the algal community changes with stratification and clays settle out of the plankton, these two species decline in abundance.

A second group of planktonic ciliates appear to exploit localized high concentrations of algae, bacteria, detritus, or other ciliates. Many of the ciliates which occur during stratification are found primarily in the metalimnion. Here, bacterial concentrations ($1-3 \times 10^7 \cdot mL^{-1}$) are sufficiently high to support the growth of small bacterivorous species (the scuticociliates). In addition, several large predatory forms (the gymnostomes, *Coleps* sp., *L. magnum*) which feed on algae and other ciliates (Bick 1972a, b) also occurred in the metalimnion. The high correlations between several of these taxa (e.g. scuticociliates and *Coleps*) and both chlorophyll *a* and bacteria support the hypothesis that zones of intense algal and bacterial activity with consequent high food concentrations are the critical factor in determining the presence and abundance of these forms.

A third group of ciliates contain symbiotic algae. In Lake Oglethorpe these ciliates (*Paradileptus* sp., *Stokesia vernalis*, *Strombidium viride*, and others) and the amoeba *Difflugia* sp. were found primarily in the epilimnion. These protozoans are mixotrophic, which probably allows them to exist in the plankton at lower food concentrations than required by strictly heterotrophic protozoans.

This discussion emphasizes the role of food in determining the abundance of ciliates. Predation also influences these populations as inferred by Sorokin and Paveljeva (1972) and experimentally demonstrated by Porter et al. (1979). The relative importance of predators as regulators of distribution and abundance remains to be elucidated. Data are accumulating which indicate that planktonic ciliates are important components of many freshwater lakes (Rigler et al. 1974; Sorokin and Paveljeva 1972; Petrova et al. 1976; Pace and Orcutt 1981). The data presented in this paper suggest that the abundance and distribution of ciliates, with the exception of mixotrophic forms, is determined, in part, by food availability and concentration. Consequently, planktonic ciliates will probably be most important as grazers, nutrient regenerators, and secondary producers in more eutrophic lakes and seasonally within lakes at sites where high concentrations of appropriate resources are available.

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Aspects of Larval American Lobster (*Homarus americanus*) Ecology in St. Georges Bay, Nova Scotia

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Lobster larvae first appeared in the neuston of St. Georges Bay, N.S., in 1978 on June 22 at a surface temperature of 12.5°C. Abundances ranged from 0 to 243 × 10^3 larvae·km^{-2} throughout the larval season with a seasonal average of 22.9 ± 37.9 × 10^3 larvae·km^{-2} for the entire bay. Larval production in the bay equals the highest values reported in the literature for individual stations in nearby western Northumberland Strait. We derive the first survival estimate from larval stage I to recruits entering the fishery of 0.2–0.4%. On average 81.4, 14.1, and 4.5% of the larvae were caught within the upper 30-cm, 30- to 70-cm, and 70- to 110-cm levels beneath the sea surface, respectively. This daytime distribution of lobster larvae in the upper 110 cm is modified by cloud cover. The adult distribution in the bay and wind-driven surface drift are believed to be the two main causes of the observed large-scale horizontal patchiness. Lobster larvae have a significantly high probability of capture by our nets if patches of floating seaweed are encountered. A hypothesis is proposed that the observed small-scale patchiness of both larvae and weed is caused by Langmuir circulation.

Key words: lobster larvae, *Homarus americanus*, ecology, Langmuir circulation, recruitment, survival, Nova Scotia

HARDING, G. C., W. P. VASS, AND K. F. DRINKWATER. 1982. Aspects of larval American lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. Can. J. Fish. Aquat. Sci. 39: 1117–1129.

En 1978, les larves de homard font leur première apparition dans le neuston de la baie Georges (N.-É.) le 22 juin, alors que la température de l'eau de surface est de 12,5 °C. Leur abondance, durant la saison larvaire, varie de 0 à 243 × 10^3 larves·km^{-2}, et la moyenne saisonnière est de 22,9 ± 37,9 × 10^3 larves·km^{-2} dans toute la baie. La production larvaire à cet endroit est aussi élevée que les valeurs maximales mentionnées dans la littérature à des stations individuelles du détroit de Northumberland occidental avoisinant. Nos estimations de première survie, du stade larvaire I au stade de recrue ralliant le stock exploitable, sont de 0,2 à 0,4 %. En moyenne, 81,4, 14,1 et 4,5 % des larves sont capturées dans les 30, 30–70 et 70–110 cm de la surface. La couverture de nuages influe sur cette distribution diurne des larves dans les 110 cm supérieurs. On croit que la distribution horizontale par taches à grande échelle que l'on observe est surtout le résultat de la distribution des adultes dans la baie et de la dérive superficielle sous l'action du vent. En présence d'îlots d'algues flottantes, les probabilités de capture de larves dans nos filets sont nettement plus élevées. Nous avançons l'hypothèse que la distribution à petite échelle observée, tant des larves que des algues, résulte d'une circulation de Langmuir.

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RESEARCHERS at the Marine Ecology Laboratory of the Bedford Institute of Oceanography have been studying various ecological aspects of St. Georges Bay, N.S. (Marine Ecology Laboratory 1980), a region believed to be representative of the highly productive southern Gulf of St. Lawrence (see Dickie 1980 for fishery yields). Larval American lobster (*Homarus americanus*) production in this bay is worth studying for two reasons: first, St. Georges Bay has produced a consistently high yield to the fisheries over the past 30 yr (Statistics Canada 1949–78), and therefore recruitment should also be relatively constant; second, it is more feasible to study larval survival and production within the bay compared to nearby Northumberland Strait, because a closed anticyclonic gyre (Petrie and Drinkwater 1978) retains the planktonic larval lobster produced within the bay.

A larval survey was undertaken in 1978 to describe the

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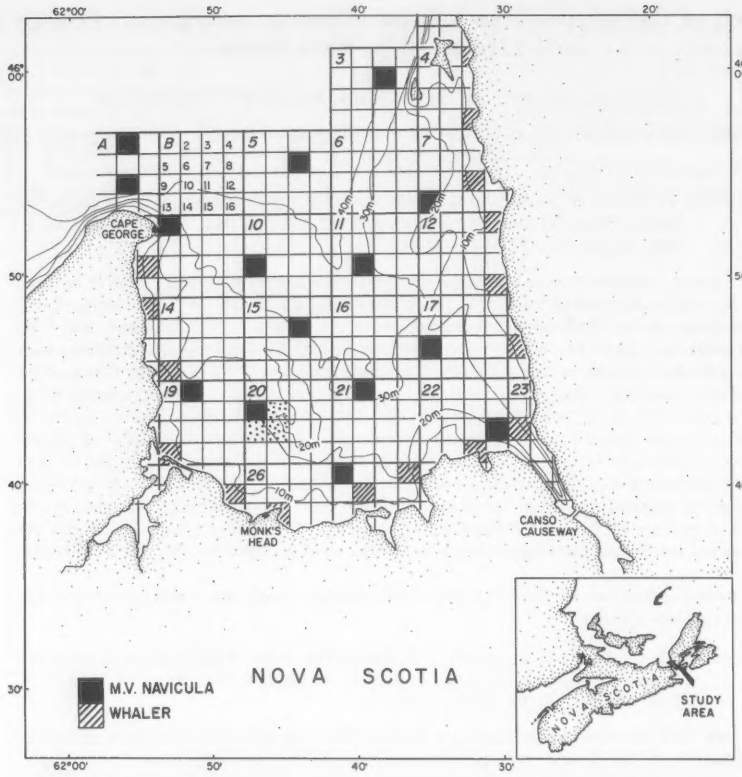

FIG. 1. Station locations on the sampling grid used for larval lobster surveys of St. Georges Bay, N.S.

seasonal and spatial distribution and evaluate the production of lobster larvae in St. Georges Bay. In a previous study both cloud cover and sampling depth were recognized as factors influencing our ability to sample adequately larval lobster populations (Harding et al. 1979). Hence, a three-compartment neuston sampler was designed and built to study the vertical structure of the larval population in the upper 110 cm. We report the production, survival, and the seasonal, vertical, and horizontal distribution of lobster larvae in St. Georges Bay in 1978; we compare our findings with previous studies done in the southern Gulf of St. Lawrence (Scarratt 1964, 1973); we evaluate previous hypotheses explaining larval lobster distribution; and we propose that Langmuir circulation can explain small-scale patchiness.

Sampling Plan and Station Locations

St. Georges Bay is ~30 × 30 km and has a mean depth of 30 m with a maximum depth of 40 m at its mouth. The bay is open on the north to Northumberland Strait and the Gulf of St. Lawrence.

Sampling sites in St. Georges Bay (Fig. 1) were chosen to provide answers to three separate questions. Sixteen nearshore, approximately equidistant regions representing the periphery of the bay were sampled for lobster larvae from June 26 to August 23 (Table 1). This was done to verify our earlier belief that the predominantly southwesterly winds in summer transport larvae with the surface layer towards the eastern shore (Harding et al. 1979). Thirteen sampling regions were chosen in the central bay to estimate larval production within the bay. These stations were sampled biweekly from May 31 to September 6. Two additional stations were located in the western entrance of the bay to provide larval abundance estimates 'upstream' in Northumberland Strait. To facilitate describing the location of these sites, the bay was divided into 29 large squares which were again subdivided into 16 squares, each being 1 square nautical mile (1853.2 m^2). Sampling area is then designated by the large square code followed by the small square as in Fig. 1 (e.g. 3–7).

At nearshore sites an Otter surface sampler (Sameoto and Jaroszynski 1969) was towed from the side of a 5-m motor boat to sample the top 30-cm sea surface. The remaining sites were sampled with a three-compartment neuston sampler which enabled us to sample discrete depths of 0–30, 30–70, and 70–110 cm (Fig. 2). This sampler was towed from a

TABLE 1. Estimated number (and stage) of lobster larvae ($\times 10^3$) under km^2 sea surface in nearshore collections, St. Georges Bay 1978, corrected because only 81.7% of lobster larvae in a 110-cm layer are caught in the 0- to 30-cm-surface layer.

	West Coast				South Coast					East Coast						
Station:	8–12	13–4	14–13	19–13	25–8	26–11	27–6	27–4	22–15	23–9	18–9	12–16	12–4	7–11	4–15	4–3
June 26	—	—	—	—	—	—	—	—	—	—	0	2.3(I)	0	0	0	0
July 4	—	—	—	—	—	—	—	—	—	15.3(I)	36.3(I)	195.2(I) 3.9(II)	31.8(I)	11.7(I)	15.6(I)	0
July 11	—	—	—	—	—	—	—	—	—	7.3(I)	7.9(I)	0	0	0	8.3(I) 2.0(II)	10.1(I)
July 18	0	0	0	0	0	0	0	31.6(I)	—	—	—	—	—	—	—	—
July 26	0	0	0	0	0	0	0	10.2(I)	—	—	—	—	—	—	—	—
Aug. 8	—	—	—	—	—	—	—	—	2.0(I)	34.4(I) 12.0(II)	4.7(I) 12.0(II) 2.4(III)	39.8(I) 37.6(II)	5.2(II)	0	4.1(I) 2.0(III)	5.1(II) 2.5(III)
Aug. 10	0	0	0	0	0	0	0	0	—	—	—	—	—	—	—	—
Aug. 21	0	1.8(IV)	2.5(I)	0	0	—	—	—	—	—	—	—	—	—	—	—
Aug. 23	—	—	—	—	—	—	—	—	2.0(III)	0	0	0	0	0	1.8(I)	0

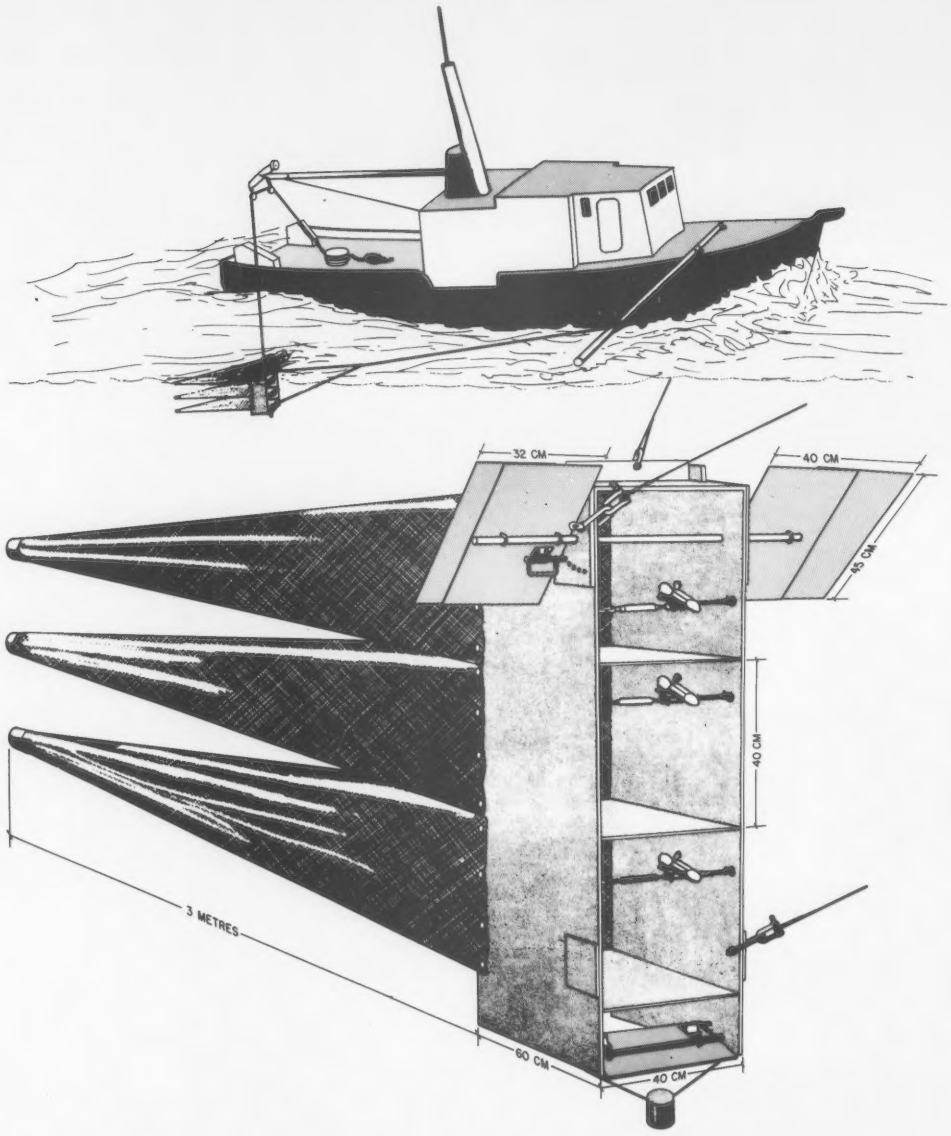

FIG. 2. Three-compartment net design and method of operation from a small boat. The angle of surface 'wings' and depressor plate is adjustable for towing depth and the size of the 'wings' is adjustable for towing from either side of the boat.

side boom on *M.V. Navicula* to keep it in undisturbed water. Both neuston samplers were towed for 1 nautical mile at ~3–4 knots. All nets had a pore size of ~520 μm, mouth aperture of 40 × 40 cm, and were equipped with General Oceanics flow meters to estimate volumes of water filtered. The top net, on average, samples the upper 30 cm of sea surface, but this is variable with sea state. Surface water temperature and cloud cover were recorded at most stations. Plankton samples were preserved in 5% buffered formalin solution and lobster larvae were later sorted, staged (Herrick 1911), and counted on shore with the aid of a desk-top magnifying lens. For comparative and computational purposes,

TABLE 2. Estimated number of stage I lobster larvae ($\times 10^3$) under km^2 sea surface, St. Georges Bay, 1978.

Station	May 31–June 1	June 22–23	July 5–6	July 19–20	Aug. 2–3	Aug. 8	August 16–17	Sept. 5–6
A–3	0	0	17.5	16.6	7.8	—	8.5	—
A–11	0	0	84.9	58.3	1.8	—	8.8	—
9–1	0	0	45.1	0	36.0	—	1.7	0
5–7	0	0	67.3	6.7	2.3	—	0	—
3–7	0	0	55.1	0	2.0	—	0	—
10–9	0	7.3	51.5	19.5	26.8	—	3.6	0
7–13	0	0	43.1	23.2	134.7	—	8.2	—
11–10	—	0	41.4	22.5	27.2	—	11.4	0
15–7	0	0	8.4	0	10.6	—	18.6	—
19–2	0	—	1.4	3.8	0	—	0	0
20–(5,6,9,10)	0	—	114.4	70.6	9.6	—	0	11.6
21–2	0	0	88.9	56.4	15.1	—	25.3	0
17–9	0	2.2	21.4	12.1	9.7	—	14.0	0
27–1	0	—	3.4	0	7.0	—	0	0
22–12	0	0	4.8	82.0	—	137.1	5.2	2.4
$\bar{x} \pm$ SD		0.8±2.1	43.2±34.7	24.8±28.0		28.5±44.8	7.0±7.7	1.6±3.9
Temp. °C		12.5±0.7	14.0±0.9	17.4±0.9		17.9±0.5	19.6±0.4	17.3±0.3

larval lobster abundances are converted to number/km^2 of sea surface.

Results

Lobster larvae first appeared as stage I in the neuston of St. Georges Bay, N.S., on June 22, 1978 (12.5 ± 0.7°C), reached peak abundance in early July, then declined until they had disappeared from the plankton by mid-September (Table 2). Larval abundance estimates ranged from 0 to 243×10^3 larvae·km^{-2} (Tables 1–3). Averaged throughout, June 22 to September 6, $22.9 \pm 37.9 \times 10^3$ larvae·km^{-2} ($\bar{x} \pm$ SD) were present in 1978.

Larval abundance was highly variable between stations on the same sampling dates (Tables 2 and 3) indicating patchiness on the order of kilometres. Floating debris, mainly eelgrass, was saved from each neuston tow taken. A predictive relationship for abundance of lobster larvae from weight of weed in the sample was not found; however, the probability of finding lobster larvae in a tow was high if the net passed through a patch of floating weed ($\chi^2 = 12.8$, $P < 0.01$; Table 4). This demonstrates that patchiness also occurred over distances of a few metres.

Eighty-one stratified tows were taken in St. Georges Bay with our three-compartment neuston sampler. A total of 753, 130, and 42 lobster larvae were caught during the summer within the 0- to 30-, 30- to 70-, and 70- to 110-cm depths, respectively (Fig. 3).

Cloud cover was recorded during 80 of these stratified tows. The total number of larvae caught in these tows are grouped at each of three depth intervals against three sky classifications; sunny, thin cloud, and total overcast (Fig. 4). During overcast conditions 95% of the larval population was present in the upper 30 cm with none captured by the lower net. On mainly sunny days 73.3, 19.2, and 7.6% of the population sampled occurred within the 0- to 30-, 30- to 70-, and 70- to 110-cm levels, respectively. Tows taken when the outline of the sun could still be seen through the clouds yielded a larval depth distribution intermediate to that found on sunny and overcast days. Interpretation of these results could be affected by the uneven occurrence of weather type throughout the sampling season, and because of the nature of the observations, statistical separation of the variables was not attempted. However, when more than one sky state occurs in the same 2-d sampling period, there is no serious disagreement with the above trend (Table 5). Time of day is not considered an important variable because all tows were taken when the sun was high (08:30–16:15).

The production of lobster larvae in the bay can be estimated using Scarratt's method (1964), extrapolating average stage duration from Templeman's (1936) laboratory determinations for environmental temperatures. The duration of stage IV larvae is taken to be one-half the experimental value because settlement is believed to occur halfway through this stage (Scarratt 1973). We improve upon Scarratt's method for estimating larval lobster survival by fitting an exponential survivor curve (Fig. 5) to our data which allows us to correct for mortality within each developmental stage. This approach has the further advantage of enabling us to calculate confidence intervals for the survival estimates. The 50% confidence intervals included in Fig. 5 demonstrates the variability inherent in

TABLE 3. Estimated number of stage II, III, and IV lobster larvae ($\times 10^3$) under km^2 sea surface, St. Georges Bay, 1978.

Station	May 31–June 1	June 22–23	July 5–6	July 19–20	Aug. 2–3	Aug. 8	August 16–17	Sept. 5–6
A–3	0	0	0	2.3 II 2.3 III	0	—	1.7 II 5.1 IV	—
A–11	0	0	0	0	5.4 IV	—	0	—
9–1	0	0	0	1.9 IV	4.0 II 4.0 III	—	6.8 IV	0
5–7	0	0	4.3 II	11.2 II	2.3 II	—	2.0 IV	—
3–7	0	0	3.0 II	25.8 II 2.8 III	2.0 IV	—	0	—
10–9	0	0	0	0	1.6 II	—	0	0
7–13	0	0	0	0	7.0 II 3.5 IV	—	1.6 IV	—
11–10	—	0	0	0	2.2 II	—	3.8 II	0
15–7	0	0	0	4.0 II	2.1 II	—	4.6 II 4.6 III	—
19–2	0	—	0	0	0	—	1.7 IV	0
20–(5,6,9,10)	0	—	4.8 II	0	0	—	1.6 IV	0
21–2	0	0	0	0	2.5 II	—	16.1 II 4.6 IV	0
17–9	0	0	0	0	0	—	5.0 II 5.0 III	0
27–1	0	—	0	0	0	—	3.2 II	0
22–12	0	0	0	0	—	90.7 II 8.4 III 6.3 IV	2.6 IV	0
$x \pm$ SD II	0	0	0.8±1.7	2.9±7.0	7.5±23.1		2.3±4.3	0
III	0	0	0	0.3±0.9	0.8±2.3		0.6±1.7	0
IV	0	0	0	0.1±0.5	1.2±2.2		1.7±2.2	0

TABLE 4. Relationship between the presence of lobster larvae and weed in a sample.

	Weed present	Weed absent
Lobster larvae present	39	40
Lobster larvae absent	11	46

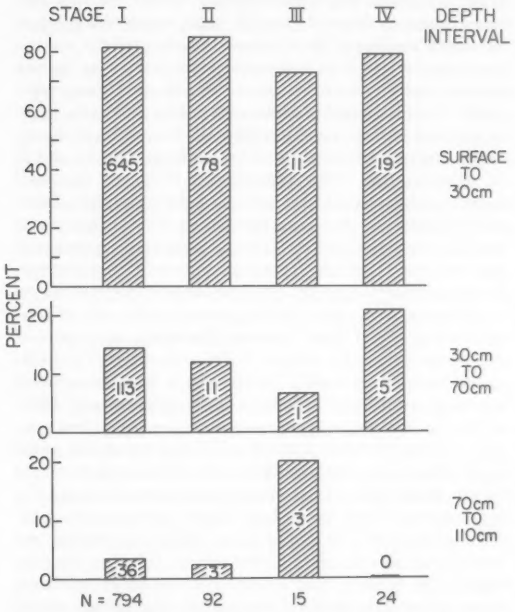

FIG. 3. Depth distribution of lobster larvae by stage in St. Georges Bay averaged throughout the summer of 1978.

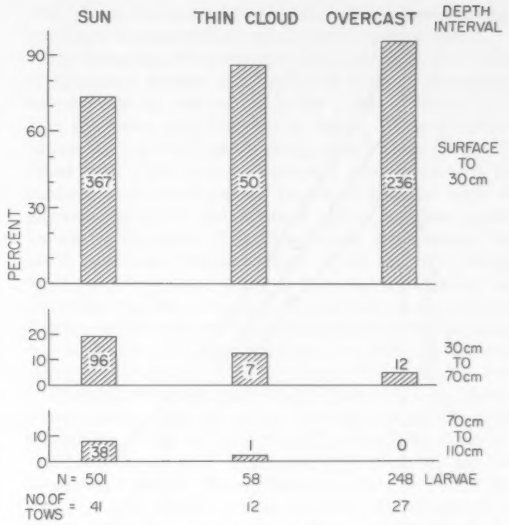

FIG. 4. The effect of cloud cover on the vertical distribution of lobster larvae in the upper 110 cm of sea surface throughout the summer of 1978 in St. Georges Bay, N.S. First column, direct sun; this category included days with scattered cumulus, but the tow was considered to be taken during sunny conditions. Second column, thin cloud; the outline of the sun could still be seen through stratus. In the third column the sun was totally obscured behind cloud.

TABLE 5. Percentage of lobster larvae in the upper net under different cloud conditions over the 1978 sampling season in St. Georges Bay.

	Sunny	Thin cloud	Overcast
June 22–23	75	—	100
July 5–6	77	—	88
July 19–20	65	83	100
August 2–3	—	93	94
August 16–17	69	84	—
September 5–6	0	—	67

any such production estimate. An estimated 367×10^6 stage I, 119×10^6 stage II, 32×10^6 stage III, and 9×10^6 stage IV lobster larvae were produced in St. Georges Bay in 1978.

Discussion

SEASONAL ABUNDANCE

The first appearance and seasonal abundance of lobster larvae in St. Georges Bay is in good agreement with earlier work done in St. Georges Bay (Harding et al. 1979) and nearby Northumberland Strait (Wilder 1953; Scarratt 1964, 1973), with the exception that the period of high abundance often continues until the middle of August in Northumberland Strait.

There are few complete seasonal studies on larval occurrence in other regions for comparison with the southern Gulf of St. Lawrence. Lund and Stewart (1970) reported an earlier first appearance of lobster larvae (June 4, 1968) in Long Island Sound, NY. These authors also found that 12.5°C was the minimum surface temperature at which larvae were present in the neuston. Lobster larvae occur as early as the middle of May off Rhode Island to as late as July along coastal Maine, but the surface temperature at first appearance was always between 11 and 13°C (Raytheon Company 1977). Therefore, the timing of first larval appearance in the plankton differs regionally, but is somehow synchronized to a narrow range of surface temperatures.

The central region of St. Georges Bay is comparable to the most productive stations in Northumberland Strait, off Richibucto Head, which averaged $20-25 \times 10^3$ larvae·km^{-2} between 1949 and 1963 (Scarratt 1964). Lund and Stewart (1970) reported an average of 1.2×10^3 larvae·km^{-2} from June to July, 1968, in Long Island Sound, NY. Unfortunately they discontinued larval sampling early in August because

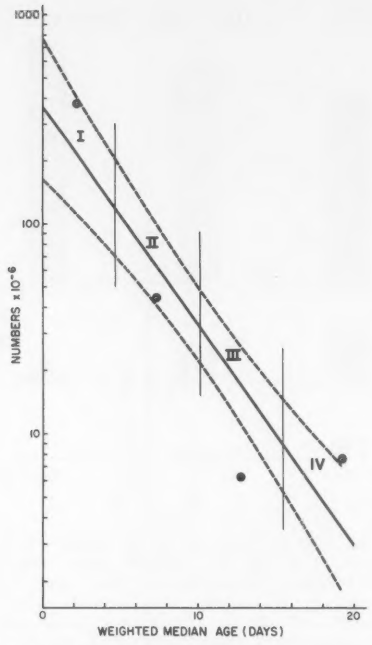

FIG. 5. Estimated survival curve for lobster larvae produced in 1978 in St. Georges Bay, N.S., showing 50% confidence intervals and the mean stage durations on the fitted exponential, $Y = 367 \times 10^6 e^{-0.24x}$, $r = 0.91$.

large numbers of ctenophores clogged their nets. Greenstein and Richter (1976) surveyed the lobster grounds at the mouth of Penobscot Bay, Maine, for larvae from June to September 1976. Conversion of their figures to per unit area results in an average of $0.2 \pm 0.4 \times 10^3$ larvae·km^{-2}. Raytheon Company (1977) surveyed four stations in Block Island Sound, RI, during 1977 for lobster larvae and reported $12.4 \pm 14.7 \times 10^3$ larvae·km^{-2} for the June to August period. The southern Gulf of St. Lawrence, therefore, appears to produce more lobster larvae per unit surface area than any other region sampled thus far.

VERTICAL DISTRIBUTION

It is generally understood that, once released by the benthic females, the four planktonic stages of the lobster inhabit the upper metre of the ocean, with few individuals reported from mid-depths (Herrick 1911; Scarratt 1973; Stasko 1980). Scarratt (1973) sampled a surface (0–60 cm) and subsurface layer (60–120 cm) for lobster larvae in western Northumberland Strait using a two-compartment net. In 21 daylight tows Scarratt found 98.3% of the larvae within the upper 60 cm. Our results give a more refined picture of larval depth distribution because we sampled narrower depth horizons. Averaged throughout the larval season, 81.4, 14.1, and 4.5% of the larvae were caught within the upper 30, 30–70, and 70–110 cm of sea surface in St. Georges Bay, respectively (Fig. 3). Stages I and II have a depth distribution which reflects this average for all planktonic stages, whereas stages III and IV were caught in too few numbers for meaningful comparisons.

Various authors have attempted to understand larval depth selection from field and experimental observations. Templeman (1937) reported large catches of lobster larvae in the surface waters of eastern Northumberland Strait on a cloudy day. Smith (1937) wrote that lobster larvae rise to the surface during the day but in darkness scatter to deeper levels. Templeman (1939) added that larvae are also concentrated at the surface during strong moonlight. Templeman and Tibbo (1945) observed that direct sunlight caused the first two larval stages to descend from the upper metre of the sea in Newfoundland bays. These authors hypothesized that a minimum light intensity is required to keep larvae near the sea surface, but above some intensity larvae seek lower light levels. They attempted to explain exceptions such as the occasional high-surface concentrations of larvae found during bright sunlight off Pictou, N.S. (Tempieman 1937), and in St. Georges Bay, Nfld. (Templeman 1939), by increased turbidity which would have reduced light penetration. Ennis (1975), however, has demonstrated in the laboratory that stage I to IV lobster larvae are more responsive to changes of pressure, with depth regulatory movements, than to changes in light intensity. Ennis did find that larvae released in the sea on dull days were stimulated to greater upward movement if released at depth, and reduced downward movement if released at the surface than on bright days. Scarratt's (1973) results from a 24-h field series with a two-compartment net support the light hypothesis of Templeman and Tibbo (1945) because larvae were more abundant in the lower net (60–120 cm) in bright sunlight and during the middle of the night. Greatest numbers of larvae were obtained in the upper 60 cm during the early morning and later afternoon when less light penetrates the sea surface. Earlier observations in St. Georges Bay, N.S. (Harding et al. 1979), demonstrated an absence of lobster larvae in the upper 30 cm on overcast nights. The present observations on cloud cover and larval depth distribution clearly document larval avoidance of full sunshine (Fig. 4). Both light intensity and hydrostatic pressure are probably important cues for larval depth selection, the former certainly appears to be important for small-scale depth adjustments near the surface. The light hypothesis of Templeman and Tibbo (1945) accommodates all our observations. Future refinement of our understanding of larval vertical distribution relative to light intensity will require an integrated measure of light in the upper metre preceding and throughout each neuston tow.

Wind-induced turbulence has also been proposed as a factor capable of modifying the vertical distribution of lobster larvae (Squires 1965, 1970; Squires et al. 1971). Our neuston tows were taken during periods of relative calm with winds of less than 15 knots. Wind may modify the vertical distribution of lobster larvae, but this has yet to be shown conclusively.

HORIZONTAL PATCHINESS

Larval lobster abundance in St. Georges Bay is highly

variable between stations (Tables 1–3). This variation can be best interpreted by analyzing the more plentiful stage I larvae (Tables 1 and 2) which individually have a short existence in the plankton.

A patchy distribution is to be expected for a relatively short-lived member of the plankton released intermittently by mobile benthic adults that select bottom type. Lobsters seek mud, sand, or gravel bottoms with occasional hard surfaces such as boulders, or even compacted mud slopes, all of which enable burrow formation (Cobb 1971; Cooper and Uzmann 1980). If the adult female distribution is adequately represented by lobster buoys during the fishing season, greatest numbers of stage I larvae should occur near banks and around the periphery of St. Georges Bay. These regions are characterized by sand–gravel and glacial–till bottoms (Kranck 1971), which are very suitable for adult lobsters. Mean drift of the surface water would appear to have little effect on larval distribution because the circulation within the bay follows a clockwise gyre with surface velocities of ~10 $cm \cdot s^{-1}$ (Petrie and Drinkwater 1978). Stage I larvae would therefore be transported a maximum of 3–5 km before the next molt is reached.

The results of our surveys indicate that further factors are involved than position of release in determining larval patchiness. High concentrations of stage I larvae occur off Cape George, in the central bay, and along the east coast (Tables 1 and 2). Few individuals were caught along the west and south coasts. This result can most simply be explained by the prevailing southwesterly winds which force water towards the eastern shore during the summer months (Drinkwater and Taylor 1979). Smith (1937), Templeman (1937), and Templeman and Tibbo (1945) have all implied that wind-driven surface currents transport lobster larvae from near the shore.

The vertical movement of larvae during daylight, as previously discussed, is probably restricted to the upper metre of the sea surface and therefore does not contribute directly to our observed variability in the horizontal plane. Caddy (1979) reinterpreted the seasonal larval lobster surveys taken in western Northumberland Strait from 1949 to 1961 (see Scarratt 1964) and found that the centers of abundance for successive larval stages I to IV moved most frequently against the prevalent southwesterly winds, as far as 20–40 km. He hypothesizes a vertical movement of larvae to greater depths during the night, which would place larvae in a presumed deep countercurrent flowing to windward. However, Caddy does not take into account the residual circulation or wind drift (e.g. a strong northwest wind could carry larvae much further than many days of light southwesterlies). Although the residual surface drift as indicated by drift bottle recoveries (Lauzier 1965) would not appear to move the larvae to the southwest, the actual wind drift may have. Too few stage III and IV larvae were caught in St. Georges Bay in 1978 to examine critically the vertical migration hypothesis of Caddy, but the catches obtained do indicate a fairly homogeneous distribution of these stages across the bay.

Larval starvation or increased vulnerability to predation could result in regional variations in survival which would also contribute to horizontal patchiness. Unfortunately, little is known about this important subject. Scarratt and Raine (1967) have shown that lobster larvae avoid adverse physical conditions such as reduced salinity in the surface water.

The foregoing discussion considers patchiness on a scale of kilometres whereas our finding of a strong association between drifting seaweed and larvae (Table 4) allows us to infer patchiness over distances of metres. Langmuir circulations occur at wind speeds greater than 6 knots (3 $m \cdot s^{-1}$) (Scott et al. 1969), and the associated water motion can be assumed to transport passive organisms laterally, such as plankton, jellyfish, and seaweed, into convergent zones known as windrows. If this mechanism is occurring, the above association between lobster larvae and free-floating weed can be explained in any of three ways. Lobster larvae can either passively concentrate in windrows along with the flotsam, maintain themselves in windrows by swimming once they are located, or actively seek windrows. All stages exhibit directional swimming vertically (Ennis 1975), thus the first two possibilities seem equally likely. Stavn (1971) has shown experimentally that zooplankters (*Daphnia magna*) can swim against the down-welling current of a simulated Langmuir spiral as long as there is a dorsal light stimulus, and the swimming speed of the organisms is equal to that of the current. Light-induced vertical migration of zooplankters in nature may cause aggregations of these organisms in convergent zones during daylight. The obvious advantages for lobster larvae to remain in windrows would be the higher food levels provided by these zooplankters. Stage IV larvae are also capable of directional swimming horizontally and would benefit from locating in convergences not only because of the supposed aggregations of food organisms, but also from concealment in and on the seaweed. In one of the rare references to floating seaweed, Normandeau Associates (1980) report that large numbers of stage IV lobster larvae were collected among drifts of salt-marsh grass. An association with seaweed would also help to explain why so many stage IV larvae are conspicuously dark red in color in contrast to the pale blue of neustonic organisms. (Ten out of 14 stage IV guts examined contained remains of *Cancer irroratus* megalops, which were also observed to concentrate near floating eelgrass.) Hence, the windrows are probably a food-rich microhabitat for lobster larvae, and the overlying seaweed may provide cover for the fourth-stage larvae. If our observed aggregations of lobster larvae and seaweed occur in windrows, future sampling should be done perpendicular to the direction of the wind, otherwise the population will be either over- or under-estimated, depending on how many windrows are sampled.

Production and Survival

Stage I ($367.3 \times 10^3 \cdot km^{-2}$) and stage II ($118.6 \times 10^3 \cdot km^{-2}$) production in St. Georges Bay is comparable to the three highest production years of 1950, 1952, and 1955 in western Northumberland Strait (Scarratt 1964, 1973). We estimate survival in the plankton from emergence to settling halfway through stage IV to be 1.0% from the fitted exponential curve (Fig. 5). Survival calculated with Scarratt's (1964) method, using the ratio of stage I to stage IV produced yields 1.9% survival, which falls within the range of values estimated for western Northumberland Strait during 1949–63

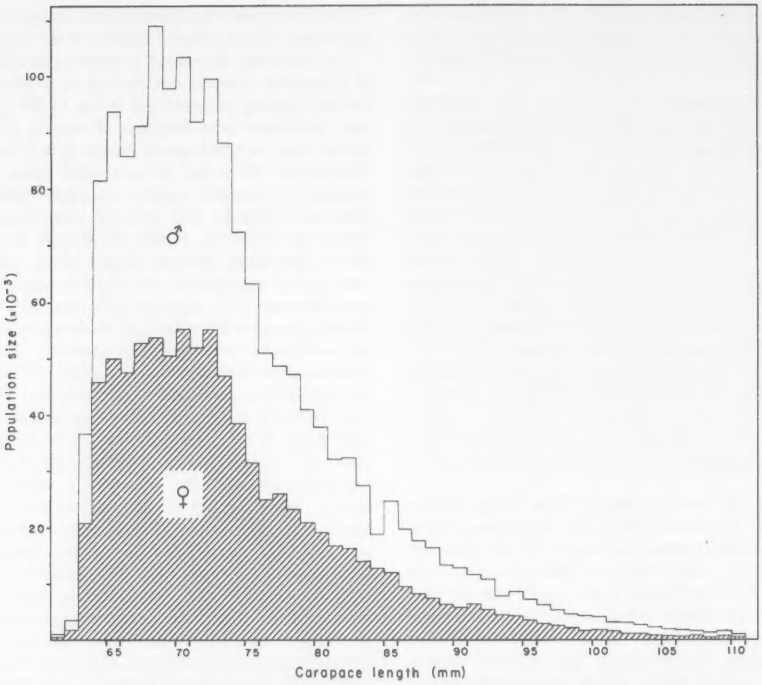

FIG. 6. Size–frequency distribution of commercial catch from port measurements taken during 1977–79 in Statistical Districts, 2, 3, 11, 12, 13, and 87 (D. Robinson personal communication) scaled to represent the average 1949–78 landing in St. Georges Bay. (Wilder's (1953) allometric equations, derived from lobsters taken near Lismore, N.S., were used for size–weight conversions.)

(Scarratt 1964, 1973).

It has not been possible in the past to estimate lobster survival from the planktonic larvae to first entry into the fishery (Anthony 1980; Campbell 1980). Two factors allow us to estimate this value for the St. Georges Bay population. Firstly St. Georges Bay supports a remarkably constant population of adults, as inferred from landings over the past 30 yr (Statistics Canada 1949–78; $549 \pm 104 \times 10^3$ kg), which suggests that larval recruitment is relatively stable from 1 yr to the next. This presumes that fishing effort has not changed during this period. Flowers and Saila (1972) have used stepwise multiple regression analysis to predict the yield of the Nova Scotian lobster fishery. They found that an effort function was of lesser importance to yield prediction than the winter water temperatures of 6–8 yr prior to recruitment and the winter temperature immediately preceding the fishing season. They attribute their findings to temperature-dependent larval mortality with an ~6 yr lag before a year-class enters the commercial catch and lower numbers of prerecruits molting into the fishery if the bottom temperature was cool. This does not prove that variable fishing effort has not had an influence (see Dow 1977), but rather that the documentation of fishing effort is too incomplete (Boudreault et al. 1977). Dadswell (1979) calculated that the number of men in the St. Georges Bay fishery (Stat. Dist. 2,3,13) has decreased from 1.3 to 0.4 men·km^{-2} of estimated fishing grounds from 1956 to 1977. However, Robinson (1979) demonstrated that the number of traps used in nearby Victoria Co., N.S., has doubled to ~225 traps per man by the late 1970s, and trap hauls per trap has increased from 25 to 35 per season on experimental grounds off Miminegash, Prince Co. If this information from the southern Gulf of St. Lawrence can be applied to St. Georges Bay, calculations indicate, from fishing intensities of 3250 trap hauls·km^{-2} in 1956 and 3150 trap hauls·km^{-2} in 1977, very little change over the period in question.

Secondly, water is believed to retain lobster larvae within the bay. The mean summer circulation of surface water within St. Georges Bay, determined by moored current metres, is a clockwise gyre. Petrie and Drinkwater (1978) demonstrated that a closed gyre in the bay could be forced by an easterly flow in Northumberland Strait. The existence of this flow in the strait has been inferred from drift bottle returns (Lauzier 1965) and limited current metre data (Farquharson 1959). A gyre in St. Georges Bay would act as a retention mechanism for larvae produced there. Even if the gyre is closed, water, and hence larvae, can be exchanged between the bay and outside through tidal or wind-driven currents. Exchange due to these causes can be expected to involve only waters in the immediate vicinity of the mouth of the bay. Larval concen-

trations just outside the bay, as measured at stations A-3 and A-11, are similar to those inside (paired t-test, $P > 0.9$), thus a net flux of larvae in or out of the bay is unlikely. A large exchange of water can take place under strong wind conditions which could lead to a net flux of larvae across the mouth of the bay. A hurricane passed over the bay in 1975 on July 28–29 producing winds up to 23 $m \cdot s^{-1}$ from the south and were in excess of 10 $m \cdot s^{-1}$ for 15 h (Petrie and Drinkwater 1978). During this period a net outflow was observed in the upper layer with compensating inflow at depth. This event may have accounted for the twofold drop in larval abundance observed on July 30–31 (Harding et al. 1979). Such events are rare and short-lived; therefore, their effect on total larval abundances throughout the season can be considered small. No such wind event occurred in 1978.

It therefore appears reasonable to compute survival rate of lobsters to first entry into the St. Georges Bay fishery from estimated stage I production in 1978 and an average annual harvest value. The average lobster landing from Fisheries Statistical Districts 3 and 13, which includes the St. Georges Bay region, is $549 \pm 104 \times 10^3$ kg spanning the years 1949–78. Lobster landings during 1978 in Statistical Districts 3 and 13 were separated by port and locality through conversation with fisheries officers and fishermen, and it was found that ~65% of the catch was trapped within St. Georges Bay. If the population in the Northumberland Strait area is about 65% exploited (DeWolf 1974), there would be an average of 549×10^3 kg of marketable lobster present during any given year in St. Georges Bay. The average number of marketable male and female lobsters in this population can be estimated from a size–frequency distribution of commercial catch in eastern Northumberland Strait scaled with the above 30-yr-average landed weight (Fig. 6).

Tagging studies done off Lismore (Wilder 1953) suggest that a 'year-class' of lobsters first enters the fishery below a carapace length (CL) of 75 mm. However, an estimate of the number of recruits entering the fishery based on the 63.5- to 75-mm-CL size group from the average size–frequency histogram neglects the possibility of lobsters either not molting or molting twice each season. It is known from recent tagging studies done off Murray Harbour, P.E.I., in eastern Northumberland Strait, that few lobsters (2% of the females, $n = 50$, and none of the males, $n = 70$; D. Robinson, Department of Fisheries and Oceans, Resource Branch, Halifax, N.S. B3J 2S7, personal communication) fail to molt past the 63.5- to 75-mm-CL size range after surviving their 1st year in the fishery. A larger number molt twice (33% of prerecruit males, $n = 69$, and 4.2% of the females, $n = 48$; D. Robinson personal communication), which means that recruits enter the fishery in the 63.5- to 87-mm-CL sizes. However, if the size–frequency distribution of prerecruit lobsters is relatively constant, as shown from experimental fishing off Maine (Krouse 1973), and the frequency of double molting in prerecruits does not change with the size of lobster, then double-molting lobsters overwintering in the ~76- to 87-mm-CL sizes will be compensated for by an equal number of double-molting recruits from a later 'year-class' that overwinters in the 63.5- to 75-mm sizes. Thus the problem of lobsters not molting or double molting does not appear to affect greatly an estimate of 1st-year recruits based on the 63.4- to 75-mm sizes from the average size–frequency diagram. This conclusion is supported by the plateau up to ~75-mm size in the size–frequency histograms for St. Georges Bay (Fig. 6).

TABLE 6. Significant correlations of larval lobster production[a] (X; number larvae produced $\cdot 3430\ m^{-2} \cdot y^{-1}$) and commercial lobster landings (Y; kg $\times 10^3$), lagged from 3 to 9 yr, in western Northumberland Strait (Stat. Dist. 82A,[b] 75, and 76) during the larval seasons of 1949–63 (Scarratt 1964, 1973). (*Significance at 0.05 level; **significance at 0.01 level; ns, not significant.)

Stage	Lag	Regression	r
I	4	$Y = 673.3+0.7X$	0.61*
	8	$Y = 719.3+0.6X$	0.52*
II	4	$Y = 744.7+4.2X$	0.66**
	8	$Y = 737.3+4.1X$	0.62*
III	4	$Y = 1013.8+6.3X$	0.46 ns
	8	$Y = 966.9+7.5X$	0.53*
IV	4	$Y = 1017.4+20.5X$	0.61*
	8	$Y = 1008.9+19.3X$	0.56*

[a]Three-year moving average used to represent merging of larval production into neighboring 'year-classes.'

[b]Stat. Dist. 82A and 82B were not separated before 1957 but approximately equal landings were reported for the following decade; therefore we used Stat. Dist. 82 divided by 2 for 1953–56.

This plateau represents $1.1 \times 10^6 \pm 18\%$ (SD) lobsters first entering the fishery where the percent standard deviation reflects the year-to-year variability of lobster landings. A survival rate of $0.30 \pm 0.05\%$, from stage I to first recruits, follows from our estimate of 367×10^6 stage I produced in 1978 (Fig. 5). However, this calculated range of survival values is too restrictive because we have not accounted for the year-to-year variation of stage I produced and the within-year sampling error. Unfortunately, the year-to-year variability in stage I production is not available for St. Georges Bay. The 1978 sampling variation in St. Georges Bay was high, ±79% (SD), which reflects the large spatial variability within the bay. However, the variation about our mean estimate from 15 stations within the center of the bay is ±20% (SD). This within-year sampling variation can be combined with the variability in the number of lobsters first entering the fishery to give a more realistic range of 0.2–0.44% for our survival estimate.

Scarratt (1964, 1973) reports stage I production values for 15 consecutive years in western Northumberland Strait which converts to ±41% (SD) variation between years. It is not surprising that the correlations between stage I larvae produced and subsequent landings as recruits 4 or 8 yr later are weak (Table 6) because the between-year variability is only twice the magnitude of the within-year variability based on our measurements in St. Georges Bay.

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Horizontal Exchange on Central Georges Bank

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An axisymmetric model of the evolution of temperature over central Georges Bank in spring, summer, and early fall is used to estimate bounds on the horizontal dispersion coefficient, K_H, consistent with the observed development of a "hot spot" in this region. We find that K_H is in the range of 150–380 $m^2 \cdot s^{-1}$, in agreement with estimates based on drogue dispersion (EG&G 1979). The effect of such a dispersion rate on passive scalars is considered for a variety of initial distributions. Although, in the absence of air–sea transfer, any initial salinity difference across the central portion of the Bank would be essentially eliminated in a few weeks, local precipitation appears to be sufficient to maintain the observed distribution. Our results indicate that maintenance of primary production at 2 g $C \cdot m^{-2} \cdot d^{-1}$ over the central portion of the Bank requires that greater than 50% of the nitrogen demand be supplied by local regeneration, assuming the Redfield ratio to be appropriate. Because exchange with off-the-Bank waters is slowest for the very center of the Bank, the supply of new nitrogen to this area should be particularly low. On the other hand, fish larvae in this area may benefit from a relatively long residence time.

Key words: horizontal exchange, Georges Bank, heat budget, nitrogen budget, residence time

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Dans le but d'estimer les liens affectant le coefficient de dispersion horizontal, K_H, correspondant à la formation d'un «point chaud» au centre du banc Georges, nous avons utilisé un modèle asymétrique de l'évolution des températures à cet endroit au printemps, en été et au début de l'automne. Nous constatons que K_H est compris dans la fourchette de 150 à 380 $m^2 \cdot s^{-1}$, ce qui est en accord avec des estimations fondées sur la dispersion de drogues (EG&G 1979). Nous analysons l'effet d'une telle dispersion sur des valeurs scalaires passives pour une variété de distributions initiales. En l'absence d'échange air–mer, toute différence initiale de salinité à la partie centrale du banc disparaîtrait normalement en quelques semaines. Cependant, les précipitations locales semblent suffisantes pour maintenir la distribution originelle. Selon nos résultats, il faut, pour maintenir la production primaire à 2 g $C \cdot m^{-2} \cdot jour^{-1}$ sur la partie centrale du banc, que 50 % de la demande en azote provienne de la régénération locale, à supposer que le quotient de Redfield soit approprié. Comme les échanges avec les eaux de l'extérieur du banc se font plus lentement au centre, les nouveaux apports d'azote dans cette région devraient être particulièrement faibles. Par ailleurs, les larves de poissons devraient profiter d'un séjour relativement long dans la région.

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THE development of a satisfactory understanding of an oceanic ecosystem, and of a capability to predict the effects of anthropogenic and environmental influences, certainly requires knowledge of the rate of exchange of water (often discussed in terms of a residence time for a region) between the system and its surroundings. The importance of ascertaining such a residence time for the water on Georges Bank, a rich fishing area on the eastern North American continental shelf, is accentuated by the recent initiation of oil and gas activity on the Bank (see Finn (1980) for some discussion) and by the seemingly (but not necessarily) contradictory sug-

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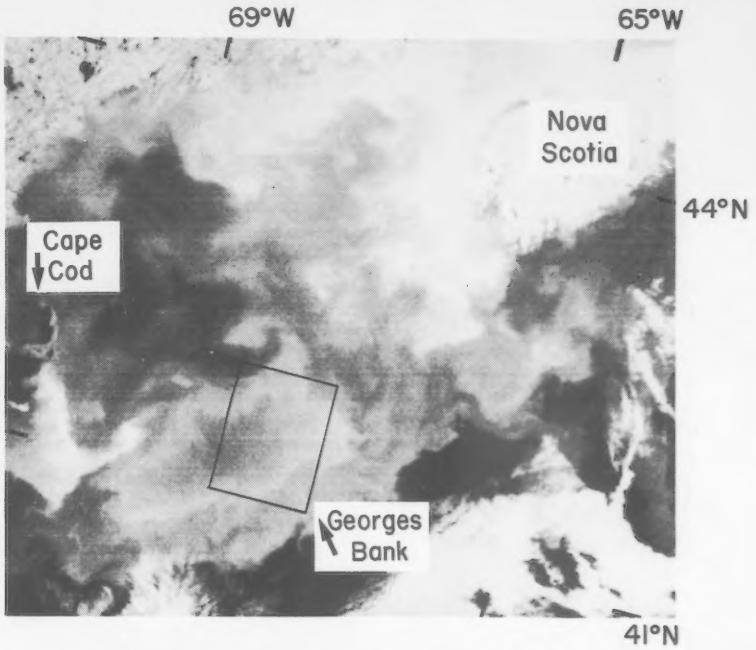

FIG. 1. NOAA-5 infrared image of the Gulf of Maine on September 5, 1978. The lighter-shaded portions of the ocean (except for clouds in the lower right-hand corner) indicate lower sea surface temperatures and the darker shades higher temperatures. The outer edge of the cool (light) band of surface water surrounding Georges Bank roughly delineates the extent of the vertically well-mixed region. We say roughly because some hydrographic sections (e.g. fig. A-56 of EG&G 1978) show the near-bottom part of the temperature front to be further up on the Bank than its surface signature. The outlined area over Georges Bank is the grid square (41−42°N, 67−68°W) for which surface heat input and sea surface temperature are shown in Fig. 3 and used in the model. (Photograph courtesy of Coastal Oceanography Division, Bedford Institute of Oceanography).

gestions that have been made with regard to physical oceanographic influences on the Bank's ecosystem. It has been suggested, on the one hand, that the high rates of primary production on the Bank in summer require some external supply of nutrients (G. A. Riley, Department of Oceanography, Dalhousie University, Halifax, N.S. B3H 4J1, personal communication; Cohen et al. 1982) while, on the other hand, a relative lack of water exchange permits enhanced survival of fish larvae (Walford 1938; G. A. Riley, personal communication; Iles and Sinclair 1982) and a permanent presence of the zooplankter *Sagitta elegans* (Redfield and Beale 1940).

Our general aim in this paper is to infer the horizontal exchange rate over central Georges Bank from a budget of a water property with known sources and sinks, and then use it in a discussion of residence time and nutrient supply. More specifically, we use a simple model of the seasonal evolution of temperature over the Bank's central shoals to estimate a horizontal dispersion coefficient and the rate of supply of nitrogen from external sources in spring, summer, and early fall.

The Georges Bank Hot Spot

In depths of less than about 50 m on Georges Bank, a state of near-vertical homogeneity in temperature and salinity is maintained year-round, primarily by tidal mixing (Bigelow 1927; Garrett et al. 1978). Within this vertically well-mixed region, satellite infrared imagery (Fig. 1) and hydrographic sections (Fig. 2) from June through September often reveal an area of higher temperature (darker shades in Fig. 1) over the Bank's central shoals. It seems likely that, away from the tidally maintained front along the perimeter of the well-mixed region, this "hot spot" arises from the increased surface heat input per unit volume (due to the decreased depth) over the center of the Bank. Another contributing factor may be the upwelling of relatively cool bottom water around the Bank's edge. A potential mechanism for such upwelling is the frictionally induced cross-frontal circulation, as in Fig. 10 of Garrett and Loder (1981).

In the next section, we make some assumptions about the horizontal exchange of heat on the central part of Georges Bank to formulate a simple mathematical model of the evo-

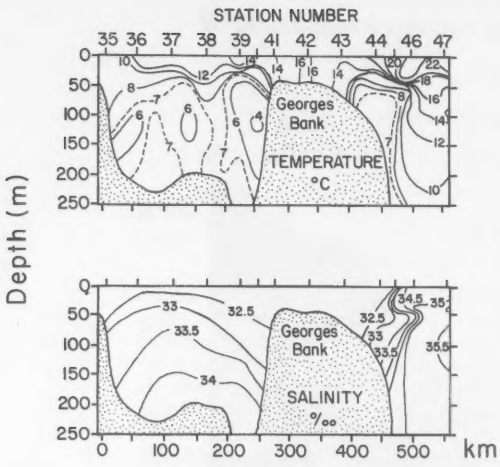

FIG. 2. Temperature and salinity sections along 67°30′W across the Gulf of Maine and Georges Bank on September 17–18, 1966. (Redrawn after Colton et al. 1968).

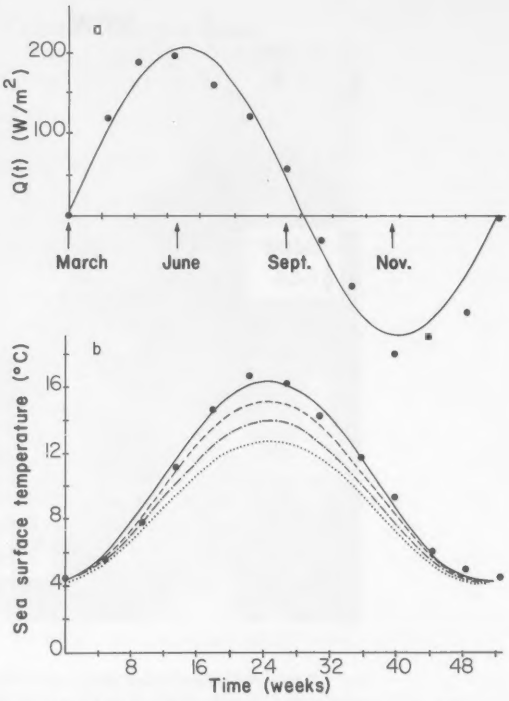

FIG. 3. Monthly values (●) of (a) surface heat input and (b) sea surface temperature averaged over many years for the 1° square 41–42°N, 67–68°W (A. F. Bunker, 1978, personal communication; for details on the calculation of surface heat input, see Bunker (1976)). The continuous curve in (a) is the least squares fit of a constant plus sinusoid to Bunker's values and is used as $Q(t)$ in (1). The solid curve in (b) is the least squares fit of a constant plus sinusoid to Bunker's temperature values, while the other curves have the amplitude of the sinusoid reduced to 0.9 (---), 0.8 (-----), and 0.7 (···) of that of the best-fitted sinusoid. These temperature curves are tested as outer boundary conditions for the temperature model. Week zero is in mid-March.

lution of the hot spot. Irrespective of the accuracy of these assumptions, however, our physical arguments that upper and lower bounds on the rate of horizontal exchange can be inferred from such a heat budget are sound. The mere existence of such a temperature anomaly suggests that horizontal mixing is not sufficient to maintain horizontal homogeneity. On the other hand, using the surface heat input data (Fig. 3a) of the late A. F. Bunker (personal communication 1978) and neglecting horizontal exchange, the expected seasonal temperature increase is about twice that observed (Fig. 3b). Thus, some horizontal exchange is necessary to account for the apparent horizontal export of heat from the top of the Bank (the suggestion, in Fig. 3, of sea surface cooling despite continued heat input in September also implies significant horizontal exchange).

A Simple Temperature Model

The primary assumptions in the model are (1) that the surface heat input to the central part of Georges Bank is spatially uniform and can be approximated by Bunker's data (averaged over many years) for the 1° square outlined on Fig. 1 (Bunker's data for the next square to the west is not significantly different); (2) that the time scale for vertical mixing is sufficiently short (a few hours) that this surface heat input can be considered to be diffused throughout the water column instantaneously, allowing the temperature to be assumed independent of depth; (3) that the depth distribution on central Georges Bank can be adequately represented as axisymmetric; and (4) that the horizontal exchange of heat, due to whatever physical processes, can be parameterized by a spatially uniform and time-independent horizontal dispersion coefficient, K_H. Assumptions (3) and (4) are rather crude approximations. Spatial smoothing of the topography over length scales of 10–15 km is implied, any drift of water across the Bank is presumed to be of secondary importance to horizontal exchange, and a geometric distortion is introduced. However, the result is a greatly simplified model which appears to be a useful first approximation to the actual situation.

Assuming zero heat flux through the sea floor, the temperature $T(r, t)$ on the central part of the Bank is then governed by the depth-averaged diffusion equation

$$(1) \qquad \frac{\partial T}{\partial t} = \frac{K_H}{rh}\frac{\partial}{\partial r}\left(rh\frac{\partial T}{\partial r}\right) + \frac{Q}{\rho C_p h}$$

where t is time, r the radial coordinate, $h(r)$ the local depth, $Q(t)$ the rate of surface heat input, ρ density, and C_p the specific heat at constant pressure.

It is important that the depth distribution in (1) be chosen so that the surface heat input per unit volume is reasonably approximated. The results in this paper are for the depth distribution in Fig. 4, determined such that the surface area inside each depth contour closely approximates that estimated

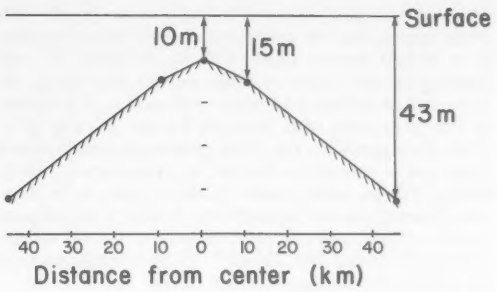

FIG. 4. Approximation to the depth distribution on central Georges Bank.

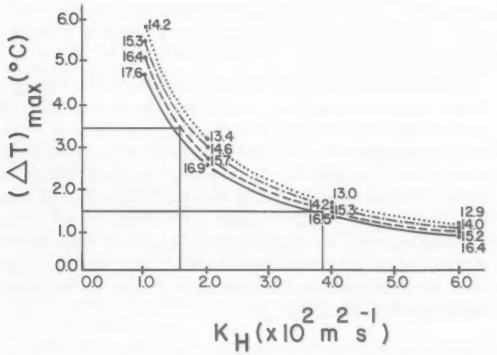

FIG. 5. Predicted maximum temperature difference $(\Delta T)_{max}$ between $r = 0$ and $r = R$ as a function of K_H with $T(R, t)$ specified to be the variations shown in Fig. 3b. Solid, dashed, dotted-dashed, and dotted curves are the results for the corresponding curves of Fig. 3b. Numbers are the maximum predicted values of the temperatures $(\bar{T})_{max}$ (°C). Observationally estimated bounds on $(\Delta T)_{max}$ and model-predicted bounds on K_H are indicated.

from bathymetric charts and checked against Fig. 2 of Hopkins and Garfield (1981). These results are not strongly dependent on the details of the choice of topography (e.g. with $h = 15$ m for $r \leq 10$ km, the results are similar). The central part of Georges Bank is thus represented by a circular region of radius $R = 45$ km whose 6360 km^2 area is only about 55% of that of the vertically well-mixed region (taken as the region with surface-to-bottom density difference less than 0.5 kg·m^{-3}) observed in August 1976 by Limeburner et al. (1978) and about 80% of that reported by Bigelow (1927). This restriction on the model's spatial extent is to avoid the vicinity of the summertime tidal front whose cross-frontal circulation probably contributes significantly to the local heat balance (Garrett and Loder 1981).

Using the approximation to Bunker's surface heat input shown in Fig. 3a, we can now solve eq. (1) (using a standard partial differential equation solver routine) for various K_H, subject to the initial condition that T is spatially uniform at the beginning of the heating season ($t = 0$), and the boundary conditions that T remains finite everywhere and that it is given

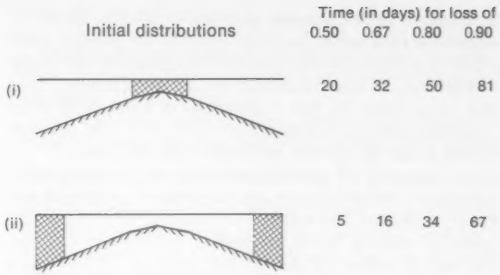

FIG. 6. Time required for the loss, from the central part of Georges Bank, of various fractions of the total initial amount of scalar for two different initial distributions. Dispersion is parameterized by a spatially uniform $K_H = 250$ m^2·s^{-1}, and the concentration at $r = 100$ km is maintained at zero.

at the model's outer boundary, $r = R$. As detailed observations of the seasonal evolution of temperature in the vicinity of the outer boundary are not available, a variety of temperature variations at $r = R$ must be considered. As first approximations, we specify $T(R, t)$ to be the best-fitted sinusoid to Bunker's sea surface temperature data for the 1° square 41−42°N, 67−68°W, and then sinusoids of the same period, phase and initial temperature, but of reduced amplitude (Fig. 3b). The results can be tested for sensitivity to phase changes in this boundary condition. $T(R, t)$ lagging those in Fig. 3b by 1 mo makes little difference, but there is greater sensitivity to a phase lead of 1 mo; however, we feel a significant phase lead to be unlikely on physical grounds. Furthermore, the uncertainty associated with possible inaccuracies in $T(R, t)$ is considerably less than that associated with our estimate of the intensity of the observed hot spot.

The model output shows the seasonal development of a "hot spot" over the top of Georges Bank with the amplitude of the temperature maximum reduced from, and phase leading, that predicted in the absence of horizontal exchange ($K_H = 0$ in (1)). The criteria used in estimating an appropriate range of values for K_H are that the maximum (summertime) temperature difference $(\Delta T)_{max}$ between the model's center and outer boundary, and the maximum spatially averaged temperature $(\bar{T})_{max}$ agree with observations. Figure 5 shows $(\Delta T)_{max}$ as a function of K_H, together with some corresponding values of $(\bar{T})_{max}$, for the choices of $T(R, t)$ shown in Fig. 3b. As expected, a high rate of horizontal exchange (large value of K_H) allows only a small temperature difference while a lower exchange rate results in a larger temperature difference. Bounding $(\Delta T)_{max}$ on the basis of observations is difficult but, using available satellite imagery and hydrographic sections, we assume a range of 1.5−3.5°C. Then, taking into consideration the values of $(\bar{T})_{max}$, we conclude from Fig. 5 that the most appropriate outer boundary variation is the sinusoid with amplitude 0.9 times that of the best-fitted sinusoid. Thus, based on Fig. 5, K_H is expected to be in the range of 150−380 m^2·s^{-1}.

Residence Times

Having obtained a quantitative estimate of the rate of horizontal exchange of heat on central Georges Bank from the

temperature model, it is now possible to estimate the rate of dispersion (and hence residence time) of any passive scalar which is dispersed by the same physical processes and whose distribution can be approximated as depth-independent. To do this, we examine the rate of dispersion of a variety of initial scalar distributions, assuming $K_H = 250\ m^2 \cdot s^{-1}$ and zero flux of that scalar through the sea surface and sea floor.

As examples of possible relevance to fish eggs, phytoplankton, immotile larvae and zooplankton, suspended sediment, pollutants, and dissolved substances, we consider (i) a spatially uniform initial distribution (of arbitrary concentration) of radius 10 km at the very top of the Bank ($r \leq 10$ km) and (ii) a spatially uniform initial distribution in a ring of width 10 km near the outer boundary of the modeled region (35 km $\leq r \leq$ 45 km). To quantify the rate of dispersion, the time required for the loss, from the central part of the Bank ($r \leq R = 45$ km), of various fractions of the total initial amount of scalar is calculated. Figure 6 shows the results assuming that depth increases into the far field at the same rate as for 10 km $< r \leq$ 45 km and, as an outer boundary condition, that zero concentration is maintained at $r = 100$ km. After some time, the rate of loss from the region of interest ($r \leq 45$ km) is dependent on these arbitrary specifications but, until the scalar reaches the area in which these specifications are made, the dispersion remains insensitive to them. For initial distributions confined to $r \leq 5$ km and $r \leq 20$ km, the calculated times differ only slightly from those for (i).

In interpreting these results in terms of a residence time, two fundamental points should be noted. Firstly, irrespective of how residence time is specifically defined, its magnitude is likely to be dependent on the initial distribution of the scalar of interest. Secondly, for the same initial distribution, the "effective" residence times of two different scalars, or different concentrations of the same scalar, may differ significantly. For example, for an initial distribution of eggs and larvae as in (i) and assuming that only 10% (a high recruitment) need remain in a desirable environment (say $r \leq$ 45 km) for a successful year-class, then the "effective" residence time is ~ 81 d. For the same initial distribution of, say, a dissolved pollutant, it is possible that the local concentration could be everywhere reduced to a harmless level after a much shorter time (even though much of the pollutant remained inside $r = 45$ km). Thus, it may be misleading to attach a single residence time to a particular region.

Regarding the implications of these calculations for Georges Bank, we emphasize that the dispersion rate inferred from the temperature model, and hence the dispersion times in Fig. 6, apply only to the central part of the Bank and only during spring, summer, and early fall. Furthermore, the uncertainty of at least 40% (and probably more; see Nitrate Supply) in our estimate of K_H results in a similar uncertainty in any estimate of residence time.

One check on the validity of the temperature model is that the inferred rate of dispersion be consistent with the observed distribution of other scalars which are dispersed by the same processes and whose sources and sinks are known. A useful physical scalar is salinity, whose summertime values on Georges Bank are often less than those of most of the surrounding waters (e.g. Colton et al. 1968 or Fig. 2; Limeburner et al. 1978). As an initial distribution of possible relevance, we consider a scalar concentration that increases linearly with r and assume that the concentration at the outer boundary ($r = 45$ km) remains fixed. With $K_H = 250\ m^2 \cdot s^{-1}$ and ignoring salt and vapour exchange with the atmosphere, the concentration difference between $r = 0$ and $r = R$ is reduced to 37% of its initial value after only 9 d and 14% after 20 d. Thus, the suggestion is that, if the present parameterization of dispersion is appropriate for salt, an axisymmetric salinity minimum on the central shoals of Georges Bank can be maintained throughout the summer only if there is an adequate excess of precipitation P over evaporation E. The salinity field $S(r)$ resulting from a given $P-E$ can be estimated from the steady-state analogue (for salt) of (1):

$$(2) \qquad 0 = \frac{K_H}{rh}\frac{\partial}{\partial r}\left(rh\frac{\partial S}{\partial r}\right) - \frac{(P-E)S}{h}$$

For uniform $P-E$, and weak horizontal gradients in S,

$$(3) \qquad S(r) \approx S(0)\left[1 + \frac{(P-E)}{2K_H}\int_0^r \frac{r'}{h(r')}\,dr'\right].$$

Climatological information on precipitation over Georges Bank is not available but, considering the precipitation at nearby land stations along with Bunker's estimates of negligible evaporation over the Bank in summer, we estimate $P-E$ to be about 110 mm/mo. For the present representation of depth and dispersion on central Georges Bank, (3) then suggests a salinity decrease of about 0.1‰ from $r = 45$ km to the Bank's center. We note, however, that it is possible for the decrease to be greater than this if fresh water can be brought onto the central part of the Bank by a process not involving significant heat exchange.

Physical Mechanisms

The values of the horizontal dispersion coefficient inferred from the temperature model are of the same order as the 100–400 $m^2 \cdot s^{-1}$ values obtained by EG&G (1979) from an analysis of the dispersion of surface drogues on central Georges Bank. It is instructive to inquire into the physical processes that contribute to this dispersion.

Neither a slow continuous drift of water over the Bank nor an episodic displacement of water from its central shoals by storms or other external forces can be conclusively ruled out. The residence times calculated above could result from a cross-Bank flow of a few centimetres per second (although it is unlikely that our axisymmetric model would be appropriate if such is the case) and, based on crude dynamical and energetic considerations, we are unable to bound the mean flow to be substantially less than this. Thus, we can only point to the quasisymmetry of the temperature field in infrared and hydrographic observations (e.g. Fig. 1 and 2), and the consistency of our results with the EG&G dispersion estimates (based on the relative motion of the drogues) as being suggestive of, at most, a weak influence from such a flow during the seasons considered here.

It is possible, using existing formulae for K_H, to show that small-scale turbulence (which does much of the vertical mixing on Georges Bank) is not the dominant process causing horizontal dispersion in this area. The main source of this small-scale turbulence during summer is the M_2 tidal currents

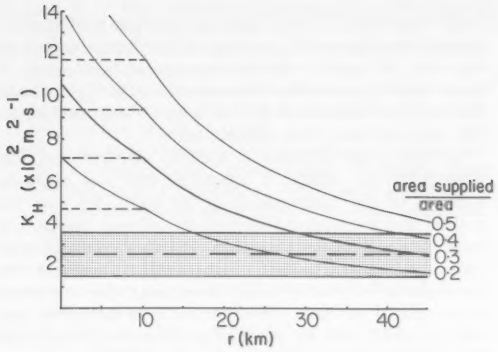

FIG. 7. Values of K_H, calculated from (4) for the nitrate distribution in (5) and the depth distribution in Fig. 4, required for the diffusive transport of nitrate to supply 0.2, 0.3, 0.4, and 0.5 of 1 mg at $N \cdot m^{-2} \cdot h^{-1}$ of nitrogen uptake inside various radii. The shaded area indicates the range of values for K_H inferred from the temperature model.

which, on the central part of the Bank, have an associated $u_* h$ in the range of 1.0−1.5 $m^2 \cdot s^{-1}$ (Greenberg 1979), where u_* is the average (over a tidal period) bottom friction velocity. The K_H for dispersion by this turbulence alone should be no more than of order $u_* h$ (Fischer et al. 1979) and that for vertical shear dispersion — the effective horizontal exchange due to vertical shear in the tidal currents acting in conjunction with vertical turbulent mixing — no more than 25 $u_* h$ (Bowden 1965).

There is, however, a secondary tidal phenomenon which can apparently account for the observed rate of dispersion on central Georges Bank, where the bottom topography is dominated by a series of sand ridges (length scales of the order of 10 km). Rectification of tidal currents is expected to result in mean Eulerian "eddies" around such sand ridges (e.g. Zimmerman 1980), and there can be a Stokes drift associated with the tidal movement of water columns in the presence of these eddies. For an irregular topography, Zimmerman (1976) has used a theory of "tidal random walk" to determine the effective dispersion coefficient for this process. Substitution of tidal and topographic parameters into his complicated and rather sensitive formulae gives values for K_H of up to several hundred $m^2 \cdot s^{-1}$ on central Georges Bank (see Garrett (1982) for more discussion).

There may also be a tidal random walk in eddies generated by low-frequency wind stress on water of variable depth. Residual vorticity can be produced either by torques due to the curl of wind stress/depth, or by the stretching of vortex tubes as the wind-generated current flows over bottom topography. Assuming a steady-state balance between the production of residual vorticity and its dissipation by bottom friction, we estimate that wind speeds on the order of 15−20 m/s would be required for either mechanism to produce mean eddies of the same strength as those expected from tidal rectification on the central shoals of Georges Bank. Thus, significant contributions from wind-generated eddies should be limited to the occasional storm. During late fall, winter, and early spring, storm winds are, of course, more frequent.

Nitrate Supply

Knowing the appropriate dispersion coefficient, it is possible to estimate the horizontal flux of any scalar whose spatial distribution is known locally.

The "diffusive" transport (flux times normal area) of a scalar, say some nutrient, across any isobath in an axisymmetric representation of a bank is $2\pi r h K_H \frac{\partial C}{\partial r}$ where C is the local concentration. If that nutrient is being biologically utilized at a spatially uniform rate $\dot{v}$ (per unit area), the fraction of the enclosed area in which such utilization can be wholly supported by this external supply is just

$$(4) \qquad \frac{A_s}{A} = \frac{2h K_H}{\dot{v} r} \frac{\partial C}{\partial r}.$$

Alternatively, the K_H needed to supply a fraction A_s/A of the nutrient uptake inside a given isobath can be readily determined if the nutrient distribution is known.

Recent primary production measurements (Cohen et al. 1982) suggest that the high level of productivity of about 2 g $C \cdot m^{-2} \cdot d^{-1}$ is maintained from spring until late fall on Georges Bank. For the purposes of the following discussion, we assume that a spatially uniform nitrogen uptake rate of 1 mg at $N \cdot m^{-2} \cdot h^{-1}$, based on the Redfield ratio of 16 atoms of nitrogen for every 106 atoms of carbon fixed, is appropriate to the central part of the Bank. It is clear that the wintertime store of nitrate in this area is not adequate to maintain the above level of productivity throughout the summer, unless most of the utilized nitrogen can be rapidly recycled. Pastuszak et al. (1982) observed average nitrate concentrations over Georges Bank of 6.2 and 6.7 mg at $N \cdot m^{-3}$ in December 1975 and February 1976, respectively. At a utilization rate of 1 mg at $N \cdot m^{-2} \cdot h^{-1}$, such a nitrate concentration would be taken up from the area of our temperature model in about 8 d.

The observations of Cohen et al. (1982) and Pastuszak et al. (1982) confirm that the nitrate concentrations on Georges Bank are substantially reduced in spring, summer, and fall. To examine the external supply of nitrogen to the central part of the Bank during these seasons, we presume that any nitrogen flux is largely in the form of nitrate and take the distribution of nitrate to be

$$(5) \qquad C(r) = C(R)\,(r/R)^2$$

so that there is zero concentration and zero gradient in concentration at $r = 0$. From the observations of the above investigators, the concentration $C(R)$ at the outer boundary is specified, somewhat arbitrarily, and probably an overestimate, as 4 mg at $N \cdot m^{-3}$. Figure 7 shows the K_H, from (4), required in order for the diffusive transport of nitrate to supply 0.2, 0.3, 0.4, and 0.5 of the assumed nitrate uptake inside various radii for the depth distribution of Fig. 3 (the dashed segments are for $h = 15$ m when $r \leq 10$ km, a possibility which cannot be discarded considering uncertainties in the spatial-averaging of bathymetry). An important general result here is that, over a shallow bank and for the physically plausible nutrient distribution assumed above, K_H must increase towards the bank's center to supply a fixed fraction of a spatially uniform nutrient demand from external sources.

The shaded area in Fig. 7 indicates the range of values of K_H inferred from the temperature model for central Georges

Bank. The actual uncertainty in these values exceeds this range in view of possible inaccuracies in the surface heat input, the temperature variation at the outer boundary, the assumption of axisymmetry, our estimate of the observed hot spot's intensity, and the presumption of a temporally and spatially uniform K_H. For example, the curves and numerical values in Fig. 5 are only slightly altered for K_H increasing linearly from $r = 35$ km to a value at $r = 45$ km that is twice the spatially uniform value inside $r = 35$ km. Consequently, without more information on the spatial dependence of K_H, such a simple temperature model cannot rule out the possibility of the actual K_H differing locally by, say, a factor of two from the shaded range in Fig. 7.

Likewise there is also uncertainty by a factor of two or so in the nitrate demand curves in Fig. 7, related to the choice of nitrate distribution, the assumption of a spatially uniform and continuous level of productivity, and the use of the Redfield ratio in nitrogen-limited conditions. Considering these uncertainties together with the possibility of other significant contributions to the external supply of nitrogen (such as diffusive fluxes in some form other than nitrate, or a nitrate flux associated with a physical process not parameterized by K_H, i.e. not affecting temperature), our estimates of physical dispersion are consistent with up to about 50% of the nitrogen demand on central Georges Bank in spring, summer, and early fall being externally supplied. If the nitrogen demand has not been overestimated, there is a strong suggestion that local biological regeneration must account for greater than 50% of the nitrogen supply. This is particularly true at the very center of the Bank, where the influence of external nitrogen sources is weakest, and is consistent with observations that regenerated ammonium can be efficiently taken up by phytoplankton in nitrate-poor regimes (Eppley and Peterson 1979; Harrison 1980).

Discussion

In determining the rate of water exchange in a region, three approaches are available: theory, budgets for conservative water mass properties, and observational studies (e.g. dispersion experiments and flux measurements). Our approach here has been to use a simple heat budget to estimate the rate of horizontal exchange on central Georges Bank, and point out that the result is consistent with those of theory and observation. It seems likely that a more accurate determination will require further progress in all three areas.

A few more comments on the temperature model are appropriate. Because the input parameters and criteria used in estimating K_H have involved climatological averages, the evolution of the temperature field (and maybe dispersion as well) may differ in any given year. Furthermore, the presumption of a time-independent K_H means that the dispersion rate and residence times are seasonal averages, masking the intermittency of influences such as wind. One of the most uncertain parameters in any such temperature model is the surface heat input, especially the magnitude of spatial variations in its latent and sensible components associated with spatial variations in sea surface temperature. However, Bunker's data suggests that radiational exchange is the dominant component of the surface heat flux over central Georges Bank in April–September, so we expect our assumption of spatially uniform heat input to be an adequate first approximation. In any case, the spatial variation that appears most likely to occur, namely a reduced net heat input to the hot spot, should lead to lower estimates of K_H (and hence a decreased nitrate flux onto the Bank) than obtained here.

In theory and assuming a spatially uniform heat loss through the sea surface, a wintertime cold spot might be expected on the central shoals of the Bank. We have not noticed such a persistent feature in the infrared imagery and hydrographic sections examined. However, reduced temperature differences on the Bank in winter are consistent with the likelihood of greater horizontal exchange (due to stronger winds) and of increased spatial variability in the surface heat loss (associated with the increased importance of sensible and latent heat transfer) providing a negative feedback.

Finally, it is possible to make some preliminary remarks about the compatibility of an external nutrient supply with larval "retention" on the central part ($h \leq 43$ m) of Georges Bank in spring, summer, and early fall. The rate of exchange appears to be high enough to allow a nontrivial external contribution to the nitrogen budget provided only that nitrate is continuously available at the outer edge of the shoals (an assessment of this should include an examination of horizontal exchange over the whole Bank and is beyond the scope of this paper). Considering the present uncertainty in the parameters in our models, previous suggestions about the relative importance of this external contribution are not inconsistent with our results. However, a verification of these suggestions requires more accurate biological and physical information. It is nearly certain that the observed rates of primary productivity on central Georges Bank cannot be wholly supported by the external nitrogen supply, and there is a strong suggestion that, if these productivity rates exist at the very center of the Bank, a large (greater than 50%) contribution from local regeneration is required.

Because the effective residence time of a patch of larvae will depend on its location and how this residence time is defined, it is not possible to reach a comprehensive conclusion on this point. However, for an initial patch at the center of the Bank, about 10% should remain within the 43-m isobath after 2 to 3 mo. Thus, in this instance, an effective residence time on the order of a few months is possible for the central part of the Bank alone. We point out that this does not involve any retention mechanism; this may be merely a semantic point, but the concept of purely physical retention seems rather inappropriate to such an energetic and dispersive environment.

Acknowledgments

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Fixation Shrinkage of Herring Larvae: Effects of Salinity, Formalin Concentration, and Other Factors

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HAY, D. E. 1982. Fixation shrinkage of herring larvae: effects of salinity, formalin concentration, and other factors. Can. J. Fish. Aquat. Sci. 39: 1138–1143.

The most important factors affecting the degree of larval shrinkage of Pacific herring (*Clupea harengus pallasi*) larvae during fixation are the salinity and formalin concentrations and initial larval size. In low formalin concentrations (2–5% formalin) shrinkage increased from less than 2% shrinkage at low salinities to about 10% shrinkage in seawater formalin. In high formalin concentrations (20–30% formalin) shrinkage was fairly uniform, ranging from about 3% shrinkage in low salinities to about 5% in seawater. Shrinkage in fixatives stored at 0, 5, 10, 20, and 30°C was slightly higher (1–2%) at the higher temperatures. Buffering agents and starvation had no effect on shrinkage. Small, young larvae shrank relatively more than larger older larvae.

Key words: herring larvae, fixation, shrinkage, formalin, salinity

HAY, D. E. 1982. Fixation shrinkage of herring larvae: effects of salinity, formalin concentration, and other factors. Can. J. Fish. Aquat. Sci. 39: 1138–1143.

La salinité et la concentration de formaline, ainsi que la taille initiale des larves, sont les facteurs les plus importants de rétrécissement des larves de hareng du Pacifique (*Clupea harengus pallasi*). À de faibles concentrations de formaline (formaline à 2–5 %), le rétrécissement augmente, passant de moins de 2 % à de faibles salinités à environ 10 % dans de la formaline à l'eau de mer. À de fortes concentrations de formaline (formaline à 20–30 %), le rétrécissement est passablement uniforme, s'étalant d'environ 3 % dans de faibles salinités à environ 5 % dans l'eau de mer. Le rétrécissement dans des agents fixateurs entreposés à 0, 5, 10, 20 et 30°C est légèrement supérieur (1–2 %) aux températures les plus élevées. Le rétrécissement n'est pas influencé par les agents-tampons et le jeûne. Les jeunes larves de petite taille se rétrécissent relativement plus que les larves plus âgées et plus grosses.

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LENGTHS of larval fish are routinely measured during many larval fish surveys and ichthyoplankton surveys. The purposes of size determination vary, but often are needed for estimating larval age and mortality. Sometimes lengths are examined to calculate condition factors as criteria of the nutritional status of larvae (Chenoweth 1970). Whatever the purpose for the measurement of larval lengths, shrinkage of larvae during the collection or fixation process could provide misleading results.

Shrinkage of herring larvae during fixation and storage in formalin has been described in several field and laboratory studies, but the results are inconsistent, perhaps reflecting different methodology. Stevenson (1962) reported a 2% shrinkage for young Pacific herring larvae captured at sea. Blaxter (1971) found that shrinkage of herring larvae captured in the North Sea varied between 1 and 4% after 1 wk in a 4% formalin–seawater solution and increased up to 6% after 3 mo storage. Shrinkage of laboratory reared larvae, which were first measured alive under anesthesia (MS222), was greater and ranged between 5 and 12% after 1 d of fixation. Even greater shrinkage, up to 20%, occurred when laboratory reared larvae were subjected to a simulated capture process by being held in a net under a stream of flowing water. Similar results were obtained with Pacific herring larvae (Hay 1981) when live, laboratory reared larvae were released and towed in a plankton net. Shrinkage of these larvae ranged between 13 and 17%. Much greater shrinkage (34–43%) occurred in tests where fixation of towed larvae was delayed for 15 min. Shrinkage varied between 5.7 and 8.6% in concurrent laboratory tests when larvae were placed directly into a 10% for-

TABLE 1. Reduction of salinity (‰) by dilution with formalin.

	Initial salinity, before formalin, ‰				
% formalin	0	7	15	20	27.5
2	0	6.9	14.7	19.6	27.00
5	0	6.7	14.3	19.0	26.10
10	0	6.3	13.5	18.0	24.80
20	0	5.6	12.0	16.0	22.20
30	0	4.9	10.5	14.0	19.25

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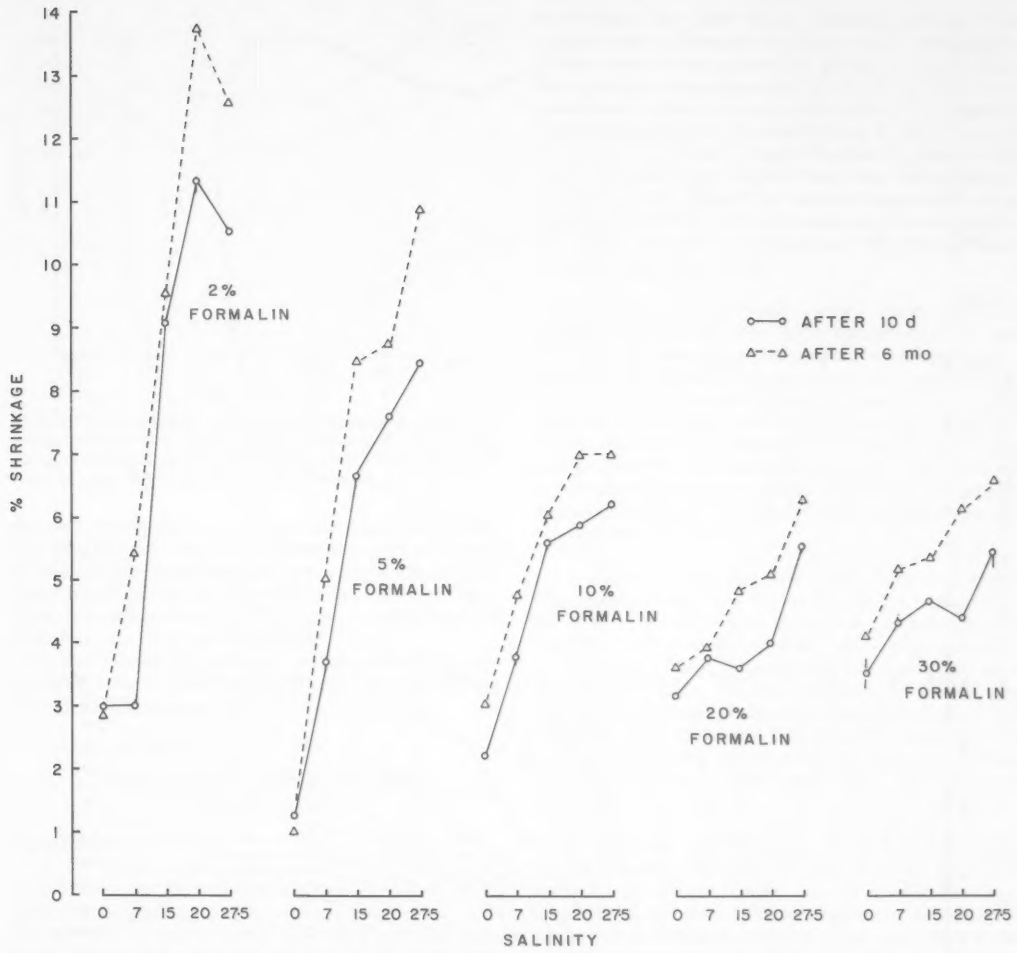

FIG. 1. Percent shrinkage of 2-wk-old larvae as a function of salinity and formalin concentration. Each point represents the mean shrinkage of a sample of 40 larvae stored for 10 d; the triangles represent shrinkage of the same group after 6 mo storage.

malin seawater solution, but it was considerably greater (29%) when larvae were killed prior to fixation in the same solution. Schnack and Rosenthal (1978) found that shrinkage of laboratory reared larvae fixed in a 4% formaldehyde seawater solution (i.e. 10% formalin) for 2 mo was about 5%, and increased with storage time. Also, they found that shrinkage was greatest in newly hatched larvae.

These studies indicate that larval shrinkage occurs in two phases: (1) a prefixation shrinkage in recently killed larvae, and (2) fixation shrinkage within the fixative. Most small larvae captured at sea with a plankton net are probably killed in the net and therefore subject to both prefixation and postfixation shrinkage, whereas laboratory reared larvae, placed alive into a fixative, would only undergo a fixation shrinkage.

This study analyzes factors affecting fixation shrinkage by comparing shrinkage in different formalin fixation solutions that varied according to salinity and formalin concentration, temperature, and the presence of pH buffering agents in the fixative. Further tests were conducted to compare shrinkage among different sizes of larvae and among larvae subjected to increasing degrees of starvation.

Materials and Methods

LARVAE

Most larvae were obtained from eggs that were fertilized, incubated, and reared in laboratory seawater (~10°C, 27.5‰). Hatching occurred about 12 d after fertilization. Feeding started about 4–5 d later when yolk sacs were mostly

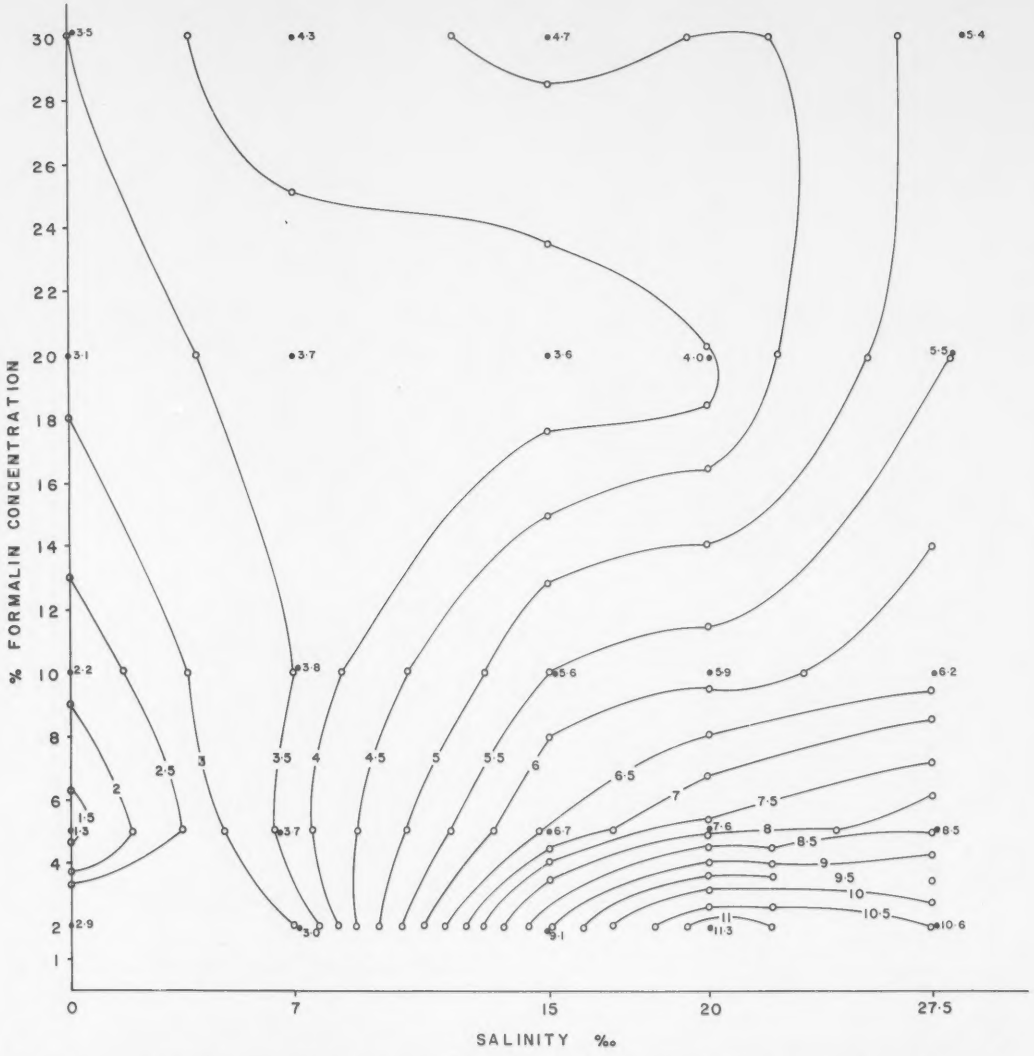

FIG. 2. Estimated isopleths of constant shrinkage as a function of salinity and formalin concentration. The open circles represent interpolated values of shrinkage (between 1.5 and 11%) for different salinity and formalin concentrations. The closed circles represent the experimental values obtained from each of the fixatives.

adsorbed. After this time, and unless they were deliberately starved, all larvae were fed daily with freshly hatched *Artemia* nauplii. For an experiment designed to compare shrinkage among different larval sizes, some larger individuals were collected alive from the water adjacent to the Pacific Biological Station (PBS) wharf where they concentrated at night under a 200-W lamp. They were removed from the water in a 1-L plastic jar and taken to the laboratory where they were held alive until used for experiments.

All measurements were made to the nearest 0.063 mm with a dissecting microscope equipped with an ocular micrometer. Live larvae were anesthetized with MS222 prior to measurement. Length was measured from the tip of the snout to the posterior end of the notochord. The smallest larvae used in any tests were about 8 mm long. Routine measurement error would be within one measurement unit (0.063 mm) so that a single 8-mm larva would have been measured to within ±0.063 mm or ±0.8%. Most larvae were 10 to 12 mm so

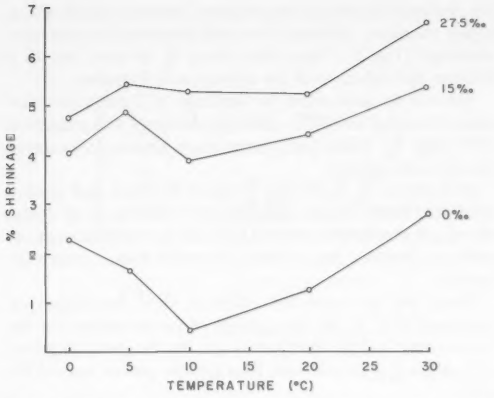

FIG. 3. Percent shrinkage of 2-wk-old herring larvae as a function of storage temperature (°C) and salinity of fixative (0, 15, 27.5‰). Formalin concentration was 10% in each solution. Each point represents the mean shrinkage of a sample of 40 larvae.

that relative measurement error would be diminished to ±0.5 to 0.6%. This error would be further reduced with estimates of mean length because positive and negative measurement errors would tend to cancel each other. In any event, maximum measurement error would be 0.8%, and this is substantially less than most treatment effects.

In most experiments shrinkage was determined by comparing the mean length of a group of larvae after fixation with their mean live length as follows:

$$\text{percent shrinkage} = \frac{(\text{mean live length}) - (\text{mean fixed length})}{\text{mean live length}} \times 100.$$

EXPERIMENTS

(i) Salinity and formalin concentration — A total of 25 combinations of salinity and formalin were used. Five initial salinities were prepared (0, 7, 15, 20, and 27.5‰) by volumetric dilution of the available seawater (27.5‰) with fresh dechlorinated tap water (0‰). Resulting salinities were checked with a salinometer. For each salinity, five different fixative solutions were prepared by adding formalin to obtain final formalin concentrations of 2, 5, 10, 20, and 30%. As a consequence of adding formalin, the resulting salinity of each fixative (except for 0‰) decreased (Table 1). Forty 2-wk-old larvae were fixed in each of the 25 fixatives for a total of 1000 larvae. First they were removed from their incubation tank, anesthetized with MS222, and measured alive before being placed in the fixative. After 10 d storage at room temperature (15–20°C), the larvae were remeasured. They were measured for a third time after ~6 mo.

(ii) Fixation temperature and salinity — Solutions of 10% formalin were prepared from initial salinities of 0, 15, and 27.5‰ by the same method described above (the actual salinities following dilution by formalin were 0, 13.5, and 24.8‰). About 100 mL from each salinity was poured into corked glass vials which were stored in five incubators set at 0, 5, 10, 20, and 30°C (i.e. a total of 15 combinations from three salinities and five temperatures). Groups of forty 2-wk-old larvae were measured alive and then placed into each vial until they were remeasured 10 d later. Control solutions were also prepared for each salinity.

(iii) Buffers — Ten percent formalin solutions prepared from initial salinities of 0, 15, and 27.5‰ (i.e. actual salinities of 0, 13.5, and 24.8‰, respectively) were buffered by saturating with calcium carbonate and sodium borate (in 27.5‰ only). Following measurement of live length under anesthesia (MS222), individual larvae (~3-wk-old) were fixed in separate small plastic petri dishes and stored for 10 d when they were remeasured. Each petri dish was sealed with parafilm and labeled so that shrinkage could be estimated from individual larva. Fifteen larvae were used in each test and control.

(iv) Starvation and shrinkage — Five identical 20-L aquaria containing seawater (27.5‰ at 10°C) were each stocked with several hundred 1-d-old (posthatching age) larvae. Food (*Artemia* nauplii) was supplied to one tank when the larvae were 5 d old, and then again every day for the duration of the experiment. Initial feeding was delayed in the

TABLE 2. Comparison of shrinkage in buffered and non-buffered fixatives; ANOVA revealed no significant differences.

Fixative solution	Salinity, ‰	Mean live length (mm) prior to fixation (n = 15)	Mean fixed length, mm (n = 15)	Percent shrinkage
Control, no buffer	0	14.29	14.13	1.18
$CaCO_3$ buffer	0	13.77	13.51	1.84
Control, no buffer	15	14.23	13.47	5.35
$CaCO_3$ buffer	15	13.79	13.10	5.00
Control, no buffer	27.5	13.70	12.97	5.33
$CaCO_3$ buffer	27.5	13.64	12.88	5.59
$NaBO_3$ buffer	27.5	13.46	12.70	5.66

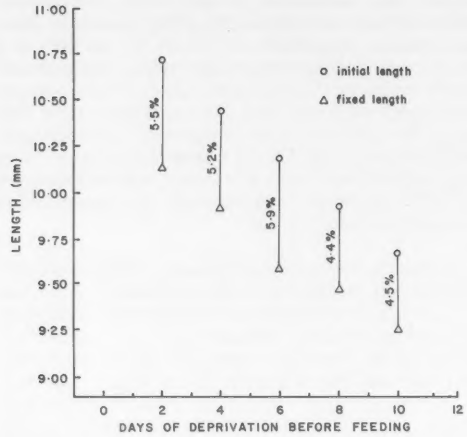

FIG. 4 Effect of starvation on larval shrinkage. The lengths of samples of 50 larvae are shown as a function of deprivation time before initial feeding. The circles represent mean lengths in millimetres prior to fixation; triangles represent fixed lengths after 10 d in a 10% formalin, 27.5‰ fixative. The lines connecting the circles and triangles show the shrinkage.

other tanks until the larvae were 7, 9, and 11 d old, respectively. One tank was never fed. After the initial feeding, larvae were fed again each day for the duration of the experiment. Because larval feeding is normally well established by 3–4 d after hatching, this feeding schedule corresponds to initial or starvation times of ~2, 4, 6, 8, and 10 d, respectively. After 10 d the experiment was stopped. Fifty larvae from each tank were removed, anesthetized, measured, and fixed in a 10% formalin–seawater (27.5‰) solution (actual salinity 24.8‰). The larvae were stored at room temperature (15–20°C) and remeasured 10 d later.

(v) Larval size and shrinkage — Four groups of 30 larvae (total 120) of different sizes and ages were used in this experiment. The three smallest groups were laboratory reared and were ~ 1, 2, and 3 wk old, respectively. The largest group was collected alive, at night, from near the PBS wharf and probably varied between 5 and 8 wk in age. The tests on each group were conducted simultaneously. Larvae were anesthetized and placed individually in small plastic petri dishes (35 × 10 mm) from which they were measured alive under the microscope. Then the labeled dishes were filled with the fixative solution (10% formalin in 27‰ seawater — actual salinity 24.8‰) and sealed with a strip of wax parafilm. Shrinkage of individual larva was determined when they were remeasured 15 d later.

Results and Discussion

Shrinkage increased with salinity in all formalin concentrations (Fig. 1). Shrinkage was least in fixatives with low concentrations of formalin and salinity, and greatest in the low-formalin, high-salinity fixatives (Fig. 2). At low salinities, increased formalin concentration increases shrinkage; at higher salinities, increased formalin concentration decreases shrinkage (Fig. 2). This latter effect is, in part, due to a dilution and reduction of the salinity with formalin.

There is no clear effect on shrinkage of fixation temperatures between 0 and 20°C, although shrinkage was greatest at 30°C (Fig. 3). Within each temperature, shrinkage increased directly with salinity.

Differences in shrinkages between buffered and control solutions (Table 2) were insignificant (ANOVA) in all cases. Shrinkage was almost identical between the buffered and nonbuffered fixatives, but, as in the previous tests, varied with salinity.

There was no consistent effect of food deprivation on shrinkage (Fig. 4): the two groups of larvae starved for the longest time had the least shrinkage, but the group deprived of food for 6 d shrunk more than the two groups starved the least.

The absolute amount of shrinkage increased directly with larval size (Fig. 5). Although the points are widely scattered, the variance due to regression is highly significant (ANOVA $F = 7.07$ with 1, df = 118, $P < 0.01$). The relative (percent) shrinkage of larvae decreases as length increases (Fig. 5). The effect is even more pronounced after 3 mo of storage.

It is clear that the salinity, formalin, and temperature variables interact. To examine further this interaction, the data from the first two experiments ((i) effect of salinity and formalin concentration; (ii) effect of temperature) were combined and examined by multiple regression analysis:

$$\begin{aligned}\%\ \text{shrinkage} = {} & 0.587 + 0.267\ (\text{salinity in ‰}) \\ & + 0.075\ (\text{temperature in °C}) \\ & + 0.049\ (\text{formalin concentration in \% by volume}) \\ & - 0.009\ (\text{salinity in ‰} \times \text{formalin concentration}).\end{aligned}$$

The regression is significant ($P < 0.01$, multiple correlation coefficient is 0.71). However, these results apply specifically to relatively small herring larvae (2 wk posthatching age) that were fixed for only 10 d. Larger older larvae would shrink less; larvae stored for longer periods would shrink more.

The likely cause of shrinkage is osmotic water loss of larvae. This is supported by the slight "negative shrinkage" of samples stored for 6 mo in low salinity and low formalin concentration. The reason for greater shrinkage in small larvae may, in part, be associated with differences in water content. Erlich (1974) showed that water content of larvae decreased with age and length. Therefore, younger smaller larvae may stand to lose relatively more water and shrink more in high-salinity fixatives.

The results apply to larvae which are immersed in the fixative alive, and may have limited application to larvae collected at sea that are killed prior to fixation. In these instances, prefixation shrinkage can be considerable (Hay 1981). Also, it is possible that prefixation shrinkage may interact with postfixation shrinkage in a nonadditive way. However, these results do apply directly to collecting or fixation circumstances where larvae are alive prior to fixation,

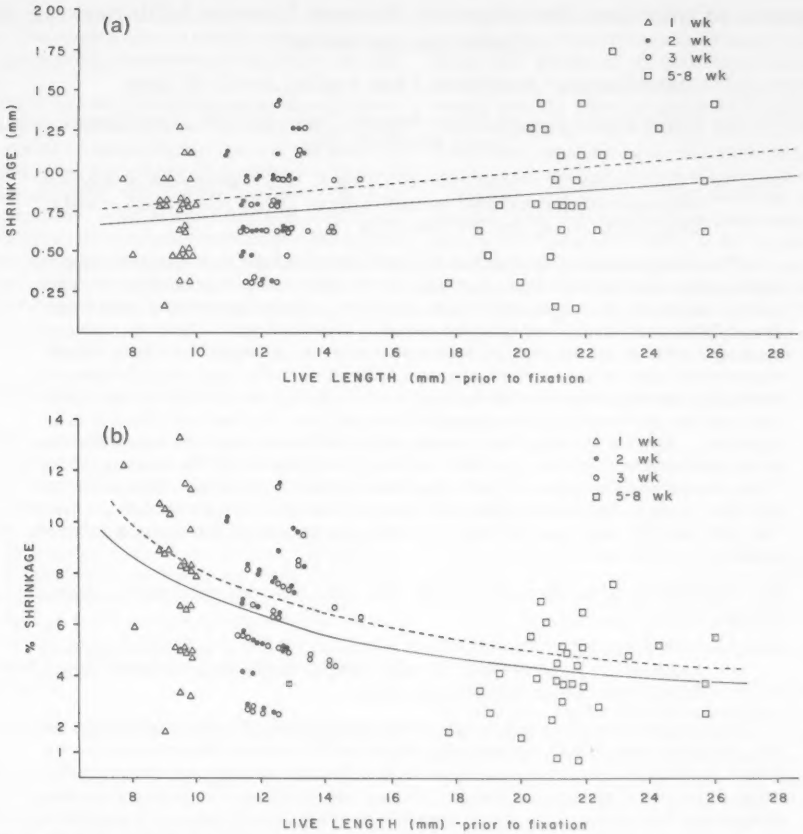

FIG. 5. (a) The effect of larval size (length in mm) on absolute shrinkage or reduction of live length in millimetres. The solid line is the fitted regression: $y = 0.564 + 0.016x$, where y is the shrinkage in millimetres and x is the initial size of the larvae. The broken line shows the same fitted regression line after storage for 6 mo. (b) The same data when shrinkage is expressed as a percentage of live length. The triangles, closed and open circles, and squares indicate, respectively, larval ages of 1, 2, 3, and 5–8 wk.

and several recommendations can be offered:

1) to minimize shrinkage, larvae should be immersed in a cool (<20°C) freshwater or low-salinity fixative with a 5–10% formalin concentration. Under these conditions shrinkage of herring larvae was less than 5% and remained low even after 6 mo of storage.

2) If fixation in freshwater is not practical, then shrinkage will be minimized by (i) reducing the salinity as much as possible and (ii) using a relatively strong formalin concentration (i.e. 10% or more).

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Pathogenesis of Infectious Hematopoietic Necrosis Virus in Adult Sockeye Salmon (*Oncorhynchus nerka*)

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MULCAHY, D., J. BURKE, R. PASCHO, AND C. K. JENES. 1982. Pathogenesis of infectious hematopoietic necrosis virus in adult sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 39: 1144–1149.

The concentration of infectious hematopoietic necrosis (IHN) virus was determined in eight organs and two body fluids from each of 60 adult sockeye salmon (*Oncorhynchus nerka*). Included in the sample were 4 males and 56 prespawning, spawning, or spent female fish. All fish were infected, and virus was present in nearly all organs. There was an overall tendency for the mean concentration to increase in many of the organs over time as the fish progressed in ripeness. In prespawning females, IHN virus could be detected in all organs and in ovarian fluid but not in serum; the incidences were highest in the gills, spleen, and pyloric ceca, and the titers were highest in the pyloric ceca and liver. Incidences of infection in the organs were higher in spawning than in prespawning females and higher still in spent females in which the incidence of virus was 100% in all organs except brains (78%) and sera (67%). Virus concentrations in organs or fluids ranged from 5 to 4.0×10^9 plaque-forming units per millilitre. In males, the highest incidences of virus were found in gills, pyloric ceca, and liver. The gills were the only organ in which the virus concentration in males exceeded that of females.

Key words: infectious hematopoietic necrosis, IHN, fish virus, viral pathogenesis, sockeye salmon

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Les concentrations du virus de la nécrose hématopoïétique (IHN) ont été déterminées sur huit organes et deux fluides corporels de chacun de 60 saumons (*Oncorhynchus nerka*) adultes. L'échantillon contenait 4 mâles et 56 femelles, ces dernières aux stades d'avant-ponte, de ponte et d'après-ponte. Tous les poissons sont infectés et le virus est présent dans presque tous les organes. À mesure qu'avance le processus de maturation, il y a tendance générale vers une augmentation des concentrations du virus dans plusieurs organes. Chez les femelles d'avant-ponte, le virus de la IHN a été détecté dans tous les organes et dans le fluide ovarien, mais non dans le sérum; l'incidence est maximale dans les branchies, la rate et les caeca pyloriques, tandis que les titres les plus élevés se trouvent dans les caeca pyloriques et le foie. L'infection est plus fréquente chez les femelles en voie de ponte que chez celles d'avant-ponte, et encore plus chez les femelles vides dont tous les organes sont infectés à 100 %, sauf le cerveau (78 %) et le sérum (67 %). Les concentrations de virus dans les organes ou les fluides varient de 5 à 4.0×10^9 unités de formation de plaques par mL. Chez les mâles, on trouve la plus forte incidence dans les branchies, les caeca pyloriques et le foie. Les branchies sont le seul organe où la concentration du virus est plus grande chez les mâles que chez les femelles.

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INFECTIOUS hematopoietic necrosis (IHN) is a lifelong virus infection (Wolf 1972; Amend 1974, 1975; Amend et al. 1973) of salmonid fishes that can be devastating to both hatchery and wild populations (Williams and Amend 1976). The virus is enzootic in virtually all populations of sockeye salmon (*Oncorhynchus nerka*) examined (Guenther et al. 1959; Amend and Wood 1972; Grischkowsky and Amend 1976). A salient feature of IHN virus infection is that the virus can generally be isolated only at the extremes of the host's life cycle, when fry or fingerlings are dying of the disease, or when the adults return to spawn. In the adults, the virus

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does not reappear until just before the fish spawn (unpublished data). This reappearance of the virus undoubtedly plays a role in egg-associated transmission of the virus to the new generation.

Knowledge of how the active disease redevelops in spawning fish can help to determine where the virus is sequestered during the period of latent infection and the mechanics of vertical transmission. Reducing or eliminating transmission is necessary for successful culture of fish populations in which the virus is enzootic. Also, efficient detection of the virus during brood stock surveys requires knowledge of the way the infection redevelops in spawning fish. In this study, we determined the incidences and concentrations of virus in various adult tissues before, during, and after spawning.

Materials and Methods

Classification of Spawning Condition

Sixty adult male and female sockeye salmon (*Oncorhynchus nerka*) returning to the Cedar River, Washington, in Fall 1980 were obtained at intervals from a hatchery fish spawning operation. Females were graded into three groups on the basis of spawning condition: prespawning, if eggs could not be expelled when slight pressure was applied; spawning, if eggs could be stripped; and spent, if spawning had already occurred and few or no eggs remained. The spawning stage of males was not determined because they were capable of repeated spawning over an extended period, and there were no easily discernible morphological criteria for such classification.

Procedure for Obtaining Samples of Organs and Fluids

As each fish was selected, it was tagged and bled from the dorsal aorta. Ovarian fluid (OF), eggs, and milt samples were taken in the field. The eggs were rinsed three times with water to remove OF. Samples and tagged carcasses were placed on ice for transportation to the laboratory.

About 1 g of tissue was aseptically removed from each of the following organs for each fish: gills (including arch), spleen, kidneys, liver, lower gut (3 cm above the anus), pyloric ceca, and brain. Each sample was weighed and stored overnight at 4°C in minimum essential medium (AutoPow, Flow Laboratories) without serum, buffered to pH 7.2 with tris(hydroxymethyl)aminomethane (MEM), and with the addition of 2.5 μg/mL amphotericin B (Fungizone, Grand Island Biological Company). Blood samples were also held overnight at 4°C, and the sera decanted.

In a separate experiment, OF and a piece of egg skein membrane were removed from each of nine spent females to determine relative levels of IHN virus. These samples were stored as described above. Differences in virus levels between the two sample types were tested for significance using Student's *t*-test ($\alpha = 0.05$).

Virus Assay

For virus titration, additional MEM was added to each tissue sample to reach a 10^{-1} dilution, and the samples were homogenized. Solids and debris were removed from all samples by centrifugation at 2000 × *g* for 10 min. The plaquing procedure described by Burke and Mulcahy (1980) was used, except that growth of all cells was at room temperature, 35-mm plates were used, and the overlay medium was supplemented with 2.5 μg/mL amphotericin B, 100 μg/mL gentamicin sulfate (Garamycin Reagent solution, Schering Corp.), 100 IU/mL penicillin, and 100 μg/mL streptomycin. The epithelioma papillosum cyprini cell line was used.

Replicate cell cultures were inoculated with sera and gonadal fluids without dilution and with serial 10-fold dilutions to 10^{-5} (sera), 10^{-6} (OF), or 10^{-3} (milt). Supernatants from the homogenized organs were put onto cell cultures without further dilution and with serial 10-fold dilutions to 10^{-5}. The cultures were incubated 7 d at 15°C before they were fixed and stained. The mean virus titer was calculated from the values (transformed to logarithms) determined for organs from individual fish. Virus titers were expressed as plaque-forming units (pfu) per gram of tissue or millilitre of fluid.

Results

Virus Incidences and Titers

The overall incidence of virus in the fish tested was 100%. Virus was isolated from all organs and fluids of males and females, except from the sera of prespawning females (Table 1). Because undiluted fish serum was toxic to the cell line, low levels ($<1 \times 10^2$ pfu/mL) of virus might not have been detected.

In prespawning females, virus was isolated most frequently from the gills, and the mean titer was highest in the liver and pyloric ceca. Except for serum, both the frequency of virus isolation and mean virus titer of each organ or fluid increased as fish passed from the prespawning stage through spawning to the spent stage. From the prespawning to the spent stage, the mean virus titer typically increased 100- to 1000-fold in each organ or fluid.

In spawning females (the stage usually sampled during routine testing of hatchery broodstocks), all fish harbored virus in OF, gills, and spleens. The frequency of virus isolation exceeded 90% for all samples except sera, kidneys, and brains. The mean virus titer was highest in the lower gut. All samples from spent females, except sera and brains, contained virus, and the mean virus titer was highest in the pyloric cecum.

Only four males were included in the study and IHN virus was found in all four fish. The frequency of virus isolation was 100% from gills, liver, and pyloric ceca (Table 1). Milt, the sample ordinarily taken for brood stock examinations, was positive in only one of the four fish, and the virus titer was only one-thousandth of the mean virus titer in the spleen, gills, lower gut, and pyloric ceca.

Levels of IHN virus varied greatly from fish to fish. The OF samples had the widest virus titer range among fish in a similar stage of spawning condition (5 pfu/mL to 1×10^9 pfu/mL in ripe fish) and the lowest and highest virus titers (5 pfu/mL in a ripe female and 4×10^9 pfu/mL in a spent female) among all the organs and fluids sampled. The range of virus titers was lowest in sera from spent females and spleens from males.

TABLE 1. Incidences, means, and ranges of IHN virus titers in organs and fluids of female sockeye salmon in three stages of spawning condition and from male sockeye salmon of indeterminate spawning condition. Titers are given as pfu/g or pfu/mL. na = not applicable.

	Prespawning females (n = 16)				Ripe females (n = 31)				Spent females (n = 9)				Males (n = 4)			
		Titer				Titer				Titer				Titer		
	Percent positive	Mean (SD)	Low	High	Percent positive	Mean (SD)	Low	High	Percent positive	Mean (SD)	Low	High	Percent positive	Mean (SD)	Low	High
Spleen	81	1.6×10^{4} (7.2×10^{1})	1.0×10^{2}	2.5×10^{7}	100	2.3×10^{5} (5.6×10^{1})	5.0×10^{2}	6.0×10^{7}	100	1.0×10^{7} (2.9×10^{1})	2.2×10^{4}	3.0×10^{8}	75	4.7×10^{6} (6.2)	5.8×10^{5}	1.5×10^{7}
Kidney	63	6.5×10^{3} (8.1×10^{1})	1.5×10^{2}	2.2×10^{7}	81	1.4×10^{5} (3.6×10^{1})	5.0×10^{2}	5.0×10^{7}	100	2.6×10^{6} (1.6×10^{1})	3.1×10^{4}	2.3×10^{7}	75	5.8×10^{4} (1.3×10^{1})	5.0×10^{3}	7.8×10^{5}
Liver	50	3.1×10^{4} (9.6×10^{1})	1.5×10^{2}	7.9×10^{7}	94	1.5×10^{5} (4.2×10^{1})	5.0×10^{2}	8.3×10^{7}	100	3.8×10^{6} (3.3×10^{1})	2.2×10^{3}	1.3×10^{8}	100	1.1×10^{5} (4.9×10^{2})	1.0×10^{2}	2.0×10^{7}
Lower gut	75	1.1×10^{4} (5.6×10^{1})	1.0×10^{2}	8.1×10^{6}	97	4.5×10^{5} (4.8×10^{1})	2.5×10^{2}	1.1×10^{8}	100	1.3×10^{7} (2.1×10^{1})	4.3×10^{3}	2.2×10^{8}	75	2.5×10^{6} (3.3×10^{1})	6.9×10^{4}	2.2×10^{7}
Pyloric ceca	56	3.0×10^{4} (1.8×10^{2})	5.0×10^{1}	1.9×10^{8}	94	2.4×10^{5} (8.5×10^{1})	1.0×10^{2}	1.9×10^{8}	100	3.2×10^{7} (4.6×10^{3})	1.5×10^{3}	3.2×10^{8}	100	2.7×10^{6} (3.6×10^{1})	1.7×10^{4}	4.0×10^{7}
Gonadal fluid	na	—	—	—	100	1.0×10^{5} (3.6×10^{2})	5.0	1.0×10^{9}	100	1.9×10^{7} (5.6×10^{2})	2.5×10^{1}	4.0×10^{9}	25	3.0×10^{3} (0)	3.0×10^{3}	—
Eggs	63	4.8×10^{3} (5.0×10^{1})	1.0×10^{2}	6.2×10^{6}	90	1.0×10^{4} (2.5×10^{1})	1.5×10^{2}	1.3×10^{7}	100	5.1×10^{5} (4.7×10^{1})	3.5×10^{2}	2.8×10^{7}	na	—	—	—
Gill	94	5.4×10^{3} (1.8×10^{1})	5.0×10^{1}	4.2×10^{5}	100	2.7×10^{5} (3.8×10^{1})	6.0×10^{2}	2.7×10^{8}	100	4.1×10^{5} (1.6×10^{1})	7.9×10^{3}	6.6×10^{7}	100	3.8×10^{6} (1.8×10^{1})	1.0×10^{5}	1.1×10^{8}
Serum	0	—	—	—	23	6.2×10^{3} (1.45×10^{1})	2.0×10^{2}	4.4×10^{5}	67	9.3×10^{3} (4.0)	2.0×10^{3}	5.0×10^{4}	25	2.0×10^{5} (0)	2.0×10^{5}	—
Brain	44	5.5×10^{2} (2.0×10^{1})	5.0×10^{1}	2.3×10^{5}	45	9.3×10^{2} (2.4×10^{1})	5.0×10^{1}	1.4×10^{7}	78	2.0×10^{3} 1.1×10^{1}	1.5×10^{2}	7.2×10^{4}	25	1.0×10^{3} (0)	1.0×10^{3}	—

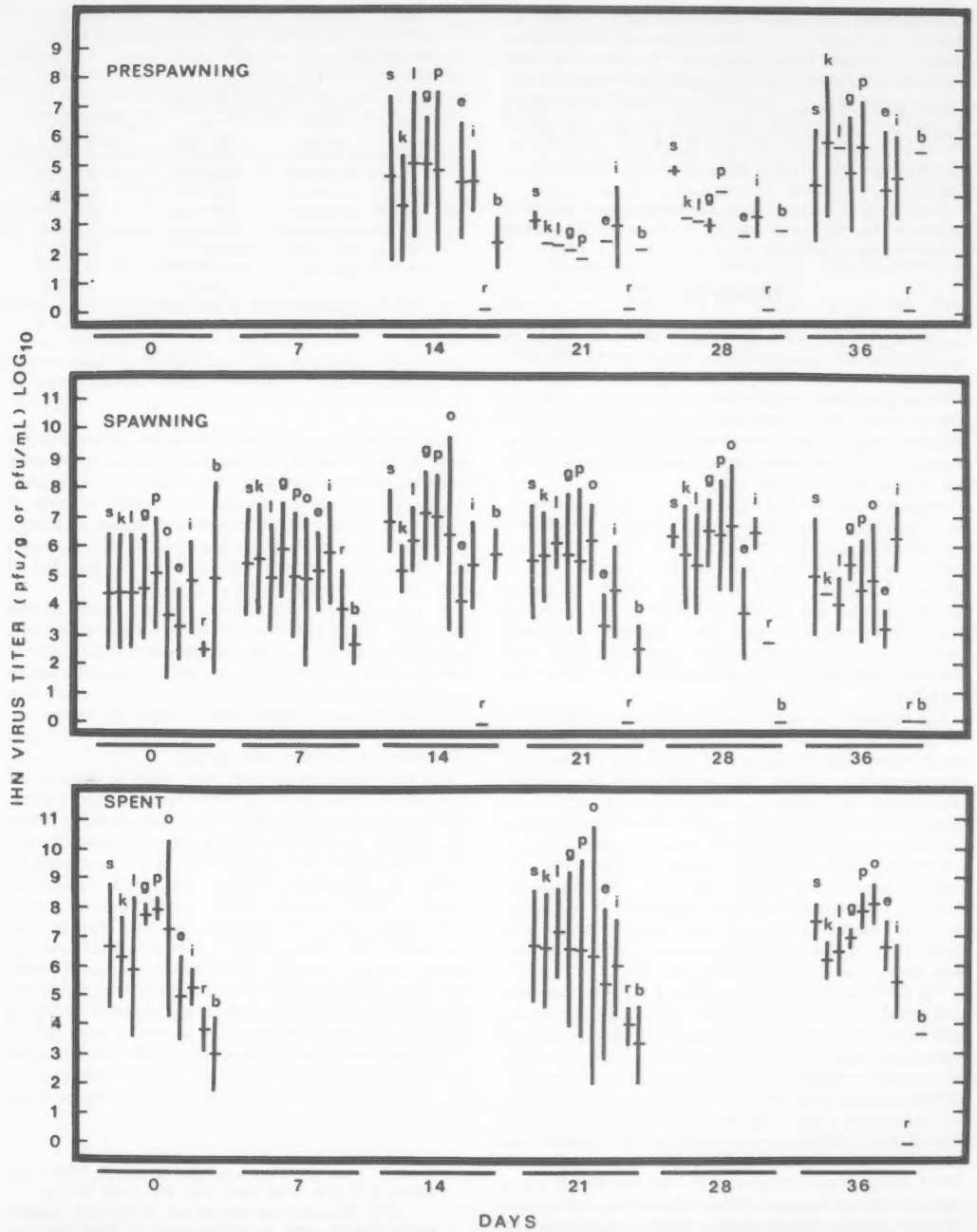

FIG. 1. Mean IHN virus titers (±1 SD) in organs and body fluids of prespawning (upper panel), spawning (center panel), and spent (lower panel) female sockeye salmon obtained on each sample day over a 36-d period. Symbols: s = spleen, k = kidneys, l = liver, g = lower gut, p = pyloric ceca, o = ovarian fluid, e = eggs, i = gills, r = serum, b = brain.

We sampled female salmon at various stages of ripeness as they became available (rather than prespawning fish first, then spawning fish, and finally spent fish). The daily mean virus titers obtained for the organs and fluids tested varied over the sample period (Fig. 1). The IHN virus titers in the visceral organs (liver, pyloric ceca, kidneys, lower gut, and spleen) varied only slightly from day to day, whereas virus titers in the fluids and non-visceral organs tended to fluctuate more widely.

Virus titers from egg skein membranes were generally slightly higher than in OF (Table 2). These apparent differences were not significant.

TABLE 2. Comparison of IHN virus titers in egg skein membranes and ovarian fluids (OF) of spawning sockeye salmon.

Fish no.	IHN virus titer: Skein (pfu/g)	IHN virus titer: OF (pfu/mL)	Titer ratios skein/OF
1	4.75×10^{3}	4.00×10^{2}	11.9
2	1.50×10^{1}	3.00×10^{1}	0.5
3	1.50×10^{1}	1.50×10^{2}	0.1
4	5.32×10^{2}	6.50×10^{1}	8.2
5	2.15×10^{2}	1.25×10^{2}	1.7
6	2.15×10^{7}	9.45×10^{7}	0.2
7	3.33×10^{8}	3.45×10^{7}	9.7
8	7.10×10^{8}	4.80×10^{8}	1.5
9	6.15×10^{5}	1.88×10^{4}	32.7
Mean	1.18×10^{8}	6.77×10^{7}	7.4

Discussion

Fish used in this study showed coloration and secondary sex characteristics associated with spawning, and IHN virus was present in every individual. In a previous study of a different population (unpublished data), we were not always able to detect virus in individual prespawning females. This difference might be due to variations in the length of time that individual fish were present on the spawning grounds, which was not controlled in either study.

The proportion of infected organs was lower in prespawning females than in spawning and spent females. Mean virus titers in the organs were also lower. Seemingly, the infection had not yet fully developed in the prespawning fish. The virus titer was higher in visceral organs than in eggs, suggesting that the primary site for the replication of the virus may not be the reproductive organs. This suggestion is supported by the low incidence and low virus titer found in the milt, compared with the high incidence and titer in the organs from male fish.

The increase in incidence and virus titers in all organs from the prespawning to the spent stage suggests that whenever possible spent fish should be used as a source of virus samples. Because of its high virus incidence and titer, ovarian fluid remain the preferred sample material. As salmon are killed to extract their eggs for hatchery use, naturally spent fish may not be available, and spawning fish must be used as a source of samples. If so, ovarian fluid still provide the best material, because of the high incidence of virus and ease of handling. Other tissues have higher mean virus titers but they are usually diluted for homogenization. Because ovarian fluid samples can be processed without dilution and homogenization, lower virus titers can be detected.

The gills were the only organ in which the mean virus titer was higher in males than in females. The mean virus titer in gills from females was very high relative to other organs, and showed the least difference in titer between ripe and spent fish of all organs sampled. In artificial infections of virus-free sockeye salmon, using waterborne virus, the gills developed and maintained a high virus titer (unpublished data). In the present study, IHN virus was present in high incidence and titer in the gills of almost every fish examined. Possibly, the 100% infection rate determined for this population was a result of both the return of lifelong virus carriers and horizontal infection of uninfected returning fish by virus released into the water from carriers. Another possible explanation is that the gills represent a true target organ for the virus as it begins to replicate in the lifelong carrier.

Fluctuations in mean virus titers of the organs over the study period are attributable to normal variations between individual animals selected each day, error due to nonrandom sampling, or insufficient sample size. Control of some of these factors would require capture and tagging of salmon entering freshwater and recapturing on the spawning grounds the fish tagged on a single day, to ensure that they had all spent the same amount of time in freshwater.

In a study of asymptomatic rainbow trout (*Salmo gairdneri*), Amend (1975) did not isolate virus from kidneys, liver, spleen, feces, or serum, but did isolate it from pyloric ceca, intestine, and OF. The virus titer in the positive viscera was 100-fold greater than that in the OF. That we found a high incidence of virus in organs found negative by Amend was probably due to use of a cell line and techniques of different sensitivity and a different host species.

The high incidences of IHN virus found in kidneys and especially in spleens are of interest as possible sources for the circulatory necrobiotic bodies previously described in salmonids infected with IHN virus (Amend and Chambers 1970; Amend and Smith 1974). Necrobiotic bodies have been described as lymphocytes (Watson et al. 1956; Amend and Chambers 1970), immature erythrocytes (Parisot et al. 1965), or karyolytic debris from disintegrating neutrophils (Amend and Smith 1974). These cells have been described in yearling sockeye salmon (Yasutake 1978), but not in adults. Correlation of virus titers in the hematopoietic tissue with numbers of necrobiotic bodies in tissue imprints and smears of circulating blood might suggest the origin and identity of these cells.

Still unknown is the residence site of IHN virus during the several-year period between the fry and spawning stages of life. The high incidence of virus in all the organs tested precluded the identification of likely organs.

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Fickian Transport and the Dispersal of Fish Larvae in Estuaries[1]

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FORTIER, L., AND W. C. LEGGETT. 1982. Fickian transport and the dispersal of fish larvae in estuaries. Can. J. Fish. Aquat. Sci. 39: 1150–1163.

We studied the regulation of ichthyoplankton dispersion in the two-layer circulation of the St. Lawrence upper estuary by determining larval abundance and vertical distribution during high frequency sampling at three stations in May, June, and July, 1979. Monthly variations in capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus harengus*) abundance were in agreement with the seasonal trends previously reported. Capelin larvae were concentrated in the surface layer, a situation which resulted in seaward drift. No significant growth was observed over the 60-d sampling period indicating continuous recruitment to, and removal from, the sampling area. Herring larvae were concentrated in the deep layer and were carried landward. The average size of herring larvae increased from the downstream to the upstream stations. Short-term fluctuations in the abundance and vertical distribution of the two species were interpreted in terms of the Fickian representation of transport for partially mixed estuaries. The major source of variation in abundance, at a given station, was the tidal advection of horizontal gradients. Capelin larvae and herring larvae smaller than 10 mm did not actively cross the pycnocline and were not submitted to the diffusive effect of the vertical current shear. The dispersal of these larvae was apparently passive. Herring larvae larger than 10 mm performed diel vertical migrations across the pycnocline and were dispersed in the horizontal plane at a faster rate than a passive contaminant of the environment. We conclude that the Fickian approach can be profitably applied to studies of dispersal and mortality of early larval stages of fish in estuaries.

Key words: ichthyoplankton, St. Lawrence estuary, dispersion, transport, vertical distribution, diel migrations, variability, abundance, tidal mixing, Fickian

FORTIER, L., AND W. C. LEGGETT. 1982. Fickian transport and the dispersal of fish larvae in estuaries. Can. J. Fish. Aquat. Sci. 39: 1150–1163.

Dans le but d'identifier les facteurs contrôlant la dispersion de l'ichtyoplancton dans un système à circulation en deux couches, des séries temporelles d'abondance et de distribution verticale ont été obtenues en mai, juin et juillet 1979 à trois stations de l'estuaire moyen du Saint-Laurent. Les variations mensuelles dans l'abondance des larves de capelan (*Mallotus villosus*) et de hareng (*Clupea harengus harengus*) correspondent à l'évolution saisonnière rapportée dans les études antérieures. Les larves de capelan, concentrées dans la couche de surface, sont entraînées vers l'aval. L'absence de croissance significative au cours des 60 jours d'observation indique un renouvellement continu de la population dans la région échantillonnée. Les larves de hareng, concentrées dans la couche profonde, sont transportées vers l'amont. La taille moyenne de cette espèce augmente d'aval en amont. Les fluctuations à court terme dans l'abondance et la répartition verticale des deux espèces sont discutées dans l'optique de la représentation fickienne du transport pour un estuaire partiellement mélangé. Les variations dans l'abondance, à une station donnée, sont dues principalement à l'advection par la marée de gradients horizontaux. Les larves de capelan et les larves de hareng de taille inférieure à 10 mm ne traversent pas activement la pycnocline et ne sont pas soumises à l'effet diffusant du gradient vertical de vitesse du courant. La dispersion de ces larves est apparemment passive. Les larves de hareng d'une taille supérieure à 10 mm effectuent des migrations circadiennes à travers la pycnocline et sont dispersées plus rapidement qu'un contaminant passif du milieu. Nous concluons que l'approche de Fick peut être appliquée avec profit à l'étude de la dispersion et de la mortalité des stades larvaires initiaux chez les stocks estuariens.

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ESTUARINE-dependent stocks of fish have developed sophisticated spawning strategies characterized by demersal eggs (Pearcy and Richards 1962; Able 1978) and temperature-dependent spawning time (Leggett 1976; Parent and Brunel 1976). It is hypothesized that these timing strategies, coupled with average conditions of estuarine circulation, maximize the number of larval fish reaching zones of high primary and secondary production, thereby maximizing survival (Pearcy 1962; Pearcy and Richards 1962; Parent and Brunel 1976; Jacquaz et al. 1977). In support of this hypothesis Turner and Chadwick (1972) reported a significant correlation between river discharge in June–July and survival of larval striped bass (*Morone saxatilis*) in the Sacramento–San Joaquin estuary. Stevens (1977) extended this relationship to the prediction of year-class strength and suggested that similar factors operated in Chesapeake Bay. Sutcliffe (1973) also reported significant correlations between discharge of the St. Lawrence River at the time of larval drift and subsequent recruitment to local fisheries of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*).

Turner and Chadwick (1972) proposed six causal mechanisms to explain the circulation–survival relationship in striped bass: flow could control recruitment by affecting (1) the distribution of larval fish, (2) the supply of detritus and nutrients, (3) the time of spawning, (4) predation on larval stages, (5) loss to diversions (important in the Sacramento–San Joaquin estuary), and/or (6) toxicity from various effluents. These mechanisms were investigated by Chadwick et al. (1977), who concluded that "outflow probably has its effect within the first two months of life, at least in part, by controlling the transport of young bass to suitable nursery areas which, in turn, influence survival through factors such as food availability." This hypothesis, formulated in an estuarine context, is in accordance with the more general match/mismatch (Cushing 1972) or critical period (Hjort 1926) hypothesis which remains popular but has proven difficult to validate empirically (May 1974).

The response of ichthyoplankton to estuarine circulation appears to be a central determinant of survival and year-class strength in estuarine spawners. A better understanding of the phenomenon of larval drift in estuaries is central to an improved ability to define and estimate the parameters of the circulation–survival relation (Graham et al. 1972; Parent and Brunel 1976).

In partially mixed estuaries, Rogers (1940), Pearcy (1962), Pearcy and Richards (1962), Graham and Davis (1971), Pearcy and Myers (1974), Able (1978), and Weinstein et al. (1980) invoked the occupation of the deep layer as a possible mechanism of landward penetration and retention of larval fish. The same argument has been used frequently to explain the retention of invertebrate larvae (see Weinstein et al. 1980 for a review). Graham (1972) suggested that larval herring maintained their position within the Sheepscot estuary by "(1) occupying the landward net tidal flow near the bottom, (2) moving upward upon reaching the limit of their landward penetration (3) then seaward in the net flow near the surface and (4) finally descending again in the landward net flow." The sampling frequency used by that author could not possibly discriminate, however, between active migrations and tide-induced vertical mixing of the larvae.

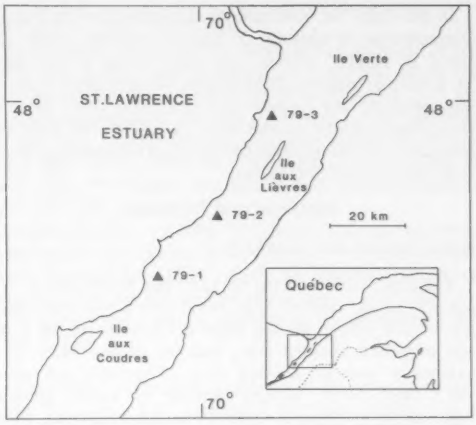

FIG. 1. Sampling locations in the St. Lawrence estuary.

In the St. Lawrence estuary, previous surveys have shown that the pelagic larvae of three commercially important species respond differently to circulation. Capelin (*Mallotus villosus*) spawn on beaches and tidal flats on both shores, and the emerging larvae are subsequently flushed out of the estuary (Jacquaz et al. 1977). Atlantic herring (*Clupea harengus harengus*) spawn demersally and the larvae are slowly carried landward from the spawning grounds located in the area of Ile Verte and Ile aux Lièvres (Tremblay 1942) toward the salt wedge in the vicinity of Ile aux Coudres (Fig. 1) (Able 1978). Rainbow smelt (*Osmerus mordax*) spawn in tributaries (Marcotte and Tremblay 1947) and the larvae, after entering the estuary, are retained in its upper reaches (Able 1978).

In a two-layer circulation these differences in fate can be accounted for by specific differences in vertical distribution. Patterns of vertical distribution leading to the retention or flushing of the larvae can result from active vertical migration triggered by tides as suggested by Graham (1972). An alternative is that early larval stages simply act as passive contaminants of the environment and are distributed by the same processes that distribute salt or temperature. In these conditions, the direction and extent of longitudinal transport would ultimately depend on the location of the spawning grounds used by each species. Larvae emerging from beaches and tidal flats would enter the circulation in the surface layer and be carried seaward at the rate of freshwater transport. Larvae emerging from the bottom in the deep layer would be transported landward by the deep countercurrent. Furthermore, if the hypothesis of passive transport is verified for a given species, then the dispersion of this species will parallel the dispersion of salt (or the dispersion of any other passive contaminant of the environment). As salt is a conservative contaminant, the divergence between the evolution of salt concentration and the evolution of larval concentration, within a given volume of water, will be a measure of larval mortality (i.e. disappearance by predation or decay after death). If these conditions can be shown to prevail, the study of early larval mortality in estuarine fishes could be materially advanced.

In this study, we examined the applicability of the Fickian representation of transport of passive properties to the dispersal of capelin, herring, and smelt larvae in the upper St. Lawrence estuary. In particular, we attempted to determine whether, and for how long, the dispersal of the early larval stages of these species is purely passive, and when and how active swimming begins to influence their ultimate large-scale longitudinal distribution.

Material and Methods

Area Studied and Sampling

The upper estuary of the St. Lawrence River (Fig. 1) is a partially mixed estuary (Muir 1980) with a two-layer circulation. The diluted surface layer is characterized by a net and important seaward flow, and the deeper saline layer exhibits a landward residual flow (d'Anglejan and Smith 1973; Meric 1975). In early summer, the salinity gradient from surface to bottom averages 10‰. Tidal amplitude varies from 2 to 6 m and the tidal currents generated can reach 250 cm/s near the surface.

In 1979, time series of larval fish abundance and vertical distribution were obtained during three sampling cruises conducted at the end of May, June, and July. On each cruise, stations 79-1, 79-2, and 79-3 with respective depths of 70, 90, and 70 m (Fig. 1) were successively occupied for 48 h or less, depending on the weather conditions. The first step of the sampling routine consisted in a current meter profile from surface to bottom at intervals of 5 m while the ship was anchored on the station. An Aanderaa recording current meter equipped with conductivity, temperature, and depth sensors was used. A 0.5-m bongo sampler equipped with opening and closing devices, flow meters, time–depth recorder, and fitted with a No. 0 (0.51 mm) and a No. 10 (0.15 mm) mesh net was then used to sample three depth-intervals (0–20, 20–40, and 40–60 m). The multiple oblique pathway of the sampler was monitored with a "Furuno" system and was controlled by varying wire length while the ship cruised at a constant speed of approximately 6.5 km/h (3.5 knots). The sampling routine was normally completed within 1.5 h and was repeated every 3 h.

Samples were preserved in 4% formalin and were completely sorted for larval herring and larval smelt. A small number of samples (<9%) containing excessive numbers of capelin larvae were subsampled with a Fulsom partitioner. In each sample, 30 randomly selected larvae were measured to the nearest 0.04 mm.

Analysis

The degree of stratification of the water column ($\hat{S}$) was estimated by integrating and averaging the vertical density profile:

$$\hat{S} = \frac{1}{n} \sum_{i=1}^{n} \Delta\sigma_{ti}\Delta z_i$$

where n is the number of pairs of adjacent measurements, $\Delta\sigma_{ti}$ is the difference in sigma-t between the ith pair of measurements, and Δz_i is the depth interval between the pair of measurements.

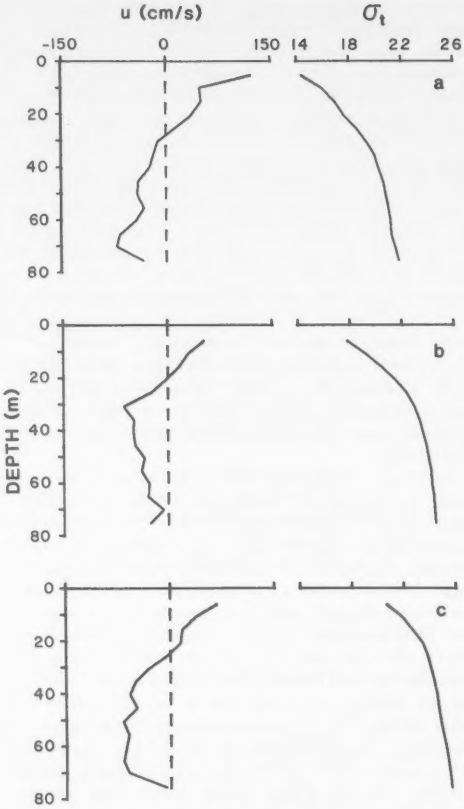

FIG. 2. Average vertical profiles of the longitudinal component of current speed (u) and water density (σ_t) integrated from late May to late July, 1979; (a) station 79-1, (b) station 79-2, (c) station 79-3. Data are averaged over one to four tidal cycles.

The stability of the water column was estimated by integrating and averaging the values of the Richardson number (Ri) calculated over each depth interval:

$$\hat{\mathrm{Ri}} = \frac{1}{n} \sum_{i=1}^{n} \frac{(g/\rho_i)\,(\Delta\sigma_{ti}/\Delta z_i)}{(\Delta u_i/\Delta z_i)^2 + (\Delta v_i/\Delta z_i)^2}$$

where g is the gravitational acceleration, ρ_i the average water density, Δu_i the difference between the longitudinal (main channel direction) component of current measured at each depth, and Δv_i the difference in the lateral (cross-channel direction) component of current measured at each depth (Fortier and Legendre 1979).

The vertical distribution of a species, at a given moment of a time series, was expressed in percentages representing the relative number of larvae captured in a given stratum. The average vertical distribution for a given station in a given month was calculated by averaging all these independent

estimates at each station. When less than one semidiurnal tidal cycle was covered by the time series or when the average larval density was less than 10/100 m^3, the resulting histogram of the average vertical distribution was left blank. The standard deviation between the percentages in each stratum was used as an index of the heterogeneity of the vertical distribution.

Short-term variations in the vertical distribution of the larvae were represented by the fluctuations in the depth of the center of mass of the distribution, Z_{cm}:

$$Z_{cm} = \sum_{i=1}^{3} p_i Z_i$$

where p_i is the proportion of larvae in the ith stratum sampled and Z_i is the mean depth of the ith stratum.

Results

Large-scale Variability

Circulation and stratification — Vertical profiles of the longitudinal component of current speed (u) indicate a two-layer circulation at all stations (Fig. 2). The mean depth of null velocity was 23.4 m. The overall surface seaward flow averaged 19.9 cm/s (17.2 km/d or 9.0 km/tidal cycle) and the compensatory landward flow averaged 18.6 cm/s (16.1 km/d or 8.4 km/tidal cycle). The corresponding vertical profiles of water density (σ_t) show that the approximated depth of the pycnocline oscillated between 20 and 25 m (Fig. 2). The mixing of freshwater from upstream to downstream is illustrated by the progressive dampening of this vertical gradient of σ_t.

Abundance — Mallotus villosus — In all months and at all stations, capelin density was one to three orders of magnitude higher than that of any other fish species. High concentrations were sustained from late May to late June. A sharp decrease occurred between late June and late July (Table 1). Although significant differences between stations ($F = 5.4, P < 0.01$), were less important than monthly variability ($F = 25.6, P < 0.001$).

Clupea harengus harengus — Herring first appeared in the collections in June and was abundant (>10/100 m^3) at the two downstream stations (79-2 and 79-3). At station 79-1, the average concentration was only 0.5/100 m^3. From late June to late July, herring densities decreased sharply at stations 79-2 and 79-3 (Table 1). Variations between stations ($F = 10.3, P < 0.001$) were smaller than monthly variations ($F = 42.3, P < 0.001$).

Osmerus mordax — Station 79-1 was the only station where larval smelt was collected in all months. The average density never exceeded 2.4/100 m^3. Again, the abundance decreased abruptly from the end of June to the end of July (Table 1). This species was virtually absent from the downstream stations in July.

Avoidance — Potential avoidance of the sampler in daylight was assessed by comparing the night-densities (number/m^3) with the day-densities for the three depth-intervals sampled. The hypothesis underlying this comparison was that if avoidance occurred, densities should be greater, on average, during darkness. In all months, the ratio of night-density over day-density oscillated around 1 (Table 2). In no case were catch rates at night significantly higher except for smelt larvae in May, in the 0- to 20 and 20- to 40-m depth-intervals ($P < 0.1$) (Table 2).

Vertical distribution — Mallotus villosus — Capelin were consistently concentrated in the top 20 m of the water column ($P < 0.05$). No clear monthly trend in this pattern was found at any station. In June, the average vertical distribution of the larvae became progressively more uniform from station 79-1 to station 79-3 (Fig. 3).

Clupea harengus harengus — In June, at stations 79-1 and 79-2, herring larvae were concentrated in the deep strata ($P < 0.05$). As with capelin, the average vertical distribution progressively became uniform from station 79-1 toward station 79-3. In July, at station 79-3, only two estimates of the vertical distribution were obtained, and the validity of the

TABLE 1. Average density (number/100 m^3, integrated over the top 60 m) of capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus harengus*), and smelt (*Osmerus mordax*) larvae, total number captured, and total volume filtered (m^3) at stations 79-1, 79-2, and 79-3 of the St. Lawrence estuary in May, June, and July, 1979. For herring and smelt larvae, the volume filtered is approximately two times larger, as the larvae captured in both nets were considered in the calculations.

	Capelin			Herring			Smelt		
	79-1	79-2	79-3	79-1	79-2	79-3	79-1	79-2	79-3
May	468.4	608.8	816.6	0.0	0.0	0.0	3.0	0.1	0.0
	27041	2125	2519	0	0	0	175	3	0
	5845	2435	1275	11924	5211	2692	11924	5211	2692
June	157.2	496.8	762.6	0.4	11.2	11.6	1.8	0.1	0.2
	14477	63550	62530	70	2368	1892	307	36	31
	8747	11685	9778	18108	23708	19746	18108	23708	19740
July	13.6	8.6	3.9	0.4	0.8	0.2	0.1	0.0	0.0
	2246	1006	10157	81	170	117	12	0	1
	10469	11310	7104	21452	22820	14251	21452	22820	14251

TABLE 2. Ratio of night-density over day-density for capelin, herring, and smelt larvae in each month for the three depth-intervals sampled (0–20, 20–40, and 40–60 m). The corresponding probability for the *t*-test between night and day catches is given in parentheses.

	Capelin			Herring			Smelt		
	0–20	20–40	40–60	0–20	20–40	40–60	0–20	20–40	40–60
May	1.59	0.42	0.61	—	—	—	3.31	4.87	0.83
	(0.37)	(0.44)	(0.66)	—	—	—	(0.09)	(0.03)	(0.85)
June	0.96	0.49	2.62	1.30	0.77	0.87	1.01	0.92	1.22
	(0.93)	(0.28)	(0.18)	(0.52)	(0.60)	(0.72)	(0.96)	(0.68)	(0.37)
July	0.30	0.23	0.80	0.58	0.93	1.50	—	—	—
	(0.08)	(0.03)	(0.73)	(0.15)	(0.87)	(0.31)	—	—	—

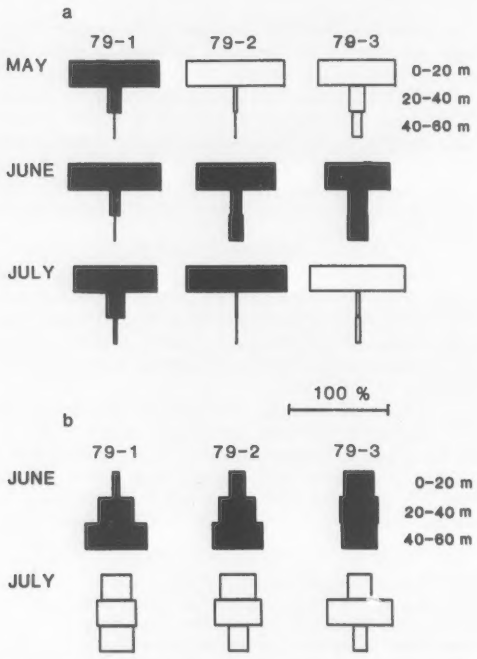

FIG. 3. Average vertical distribution: (a) capelin larvae, (b) herring larvae. The horizontal bars of the histogram represent the percentage of the total number of larvae found in a given stratum. Open histograms are approximations and may be biased because the data represent less than a full tidal cycle or because larval densities were low.

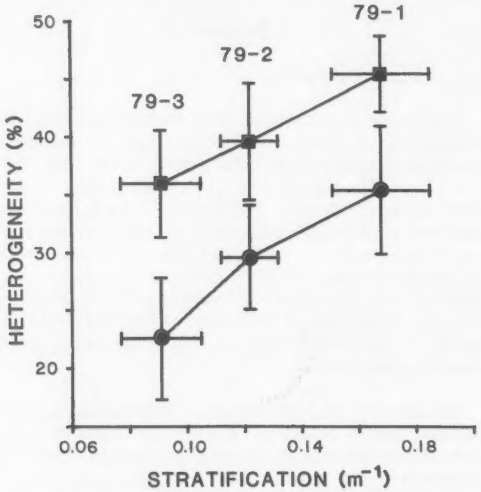

FIG. 4. Relationship between the heterogeneity of the vertical distribution and the stratification of the water column: (■) capelin larvae, (●) herring larvae. Values are averaged over three to four tidal cycles. Confidence intervals correspond to the 0.05 probability level.

average presented in Fig. 3 for this station is questionable. At station 79-2, the larvae were significantly more abundant in the middle stratum ($P < 0.01$). At station 79-1, there was no significant difference between the three strata ($P = 0.43$). No obvious trend can be seen in the variations between stations.

Osmerus mordax — Reliable estimates of the average vertical distribution of smelt larvae are available for May and July at station 79-1 where the abundances were sufficiently high. There was no significant difference in the average proportion of larvae found in each of the three strata (May, $P = 0.38$; June, $P = 0.55$; Fig. 3).

In June, with decreasing stratification of the water column from upstream (station 79-1) to downstream (station 79-3), both capelin and herring larvae tended to distribute more uniformly in the water column (Fig. 4). The confidence intervals on the values of the stratification parameter and the heterogeneity index reflect tidal variability rather than sampling imprecision.

Growth and size distribution — Mallotus villosus — Although statistically significant, differences in the average length of capelin from station to station ($F = 43.5$, $P < 0.001$) or from month to month ($F = 5.0$, $P < 0.01$) did not exceed 0.5 mm (Table 3). Except for the appearance of a few larger larvae (7–16 mm) in July at station 79-3, the distribution of sizes (Fig. 5a) remained constant over time.

Clupea harengus harengus — The average size of herring

TABLE 3. Average standard length (mm), standard deviation, and number of capelin, herring, and smelt larvae measured at stations 79-1, 79-2, and 79-3 of the St. Lawrence estuary in May, June, and July, 1979.

	Capelin			Herring			Smelt		
	79-1	79-2	79-3	79-1	79-2	79-3	79-1	79-2	79-3
May	4.65	4.76	5.09	—	—	—	8.05	5.87	—
	0.49	0.48	0.52	—	—	—	1.26	1.11	—
	569	209	200	—	—	—	175	3	—
June	4.57	4.81	4.81	7.48	7.29	7.93	12.51	13.33	10.66
	0.51	0.48	0.43	0.89	0.98	0.78	1.74	3.53	3.46
	514	1345	1063	59	881	946	291	36	20
July	4.81	4.63	4.91	15.80	10.86	11.37	16.05	—	11.68
	0.45	0.39	0.44	2.80	3.32	3.22	3.23	—	—
	554	389	779	78	167	117	12	—	1

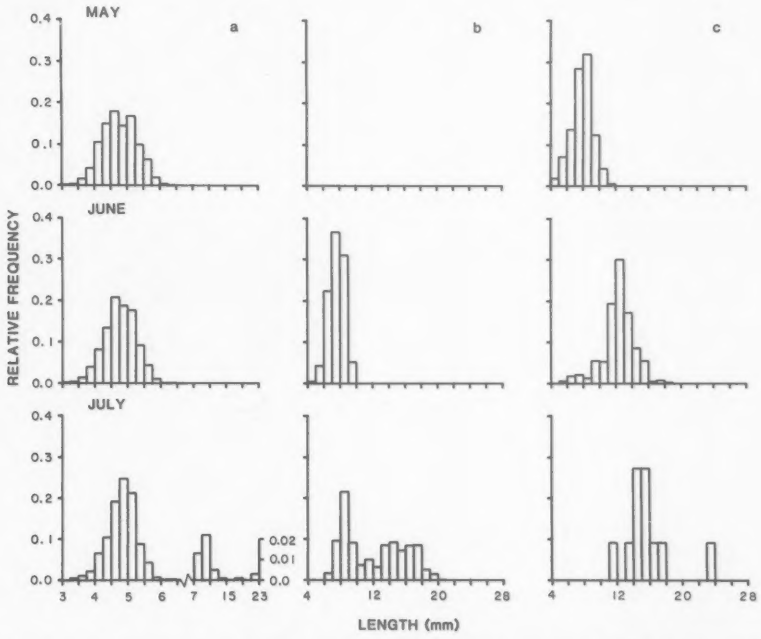

FIG. 5. Size distribution of the larvae for the 3 months sampled: (a) capelin, (b) herring, and (c) smelt larvae.

larvae varied significantly from station to station ($F = 26.6$, $P < 0.001$) but the increase in length over time (Table 3) was the predominant component of variation ($F = 380.1$, $P < 0.001$). From late June to late July, the average growth was 4.62 mm (0.15 mm/d). During that period, the distribution of sizes (integrated over space) moved to higher values, spread over a larger span, and became bimodal (Fig. 5b). This bimodality indicates the presence of two well-defined cohorts. The progressive change, from downstream to upstream, in the relative importance of these two size groups is illustrated in Fig. 6. Small larvae dominated the distribution at station 79-3 (Fig. 6a) whereas at station 79-2 the population sampled consisted of two cohorts separated at approximately 11.5 mm (Fig. 6b). The first cohort (58% of the population) was normally distributed around a modal length of 8.5 mm. The second cohort was also normally distributed with a modal length of 14.5 mm. At station 79-1, the two cohorts were completely separated and larger larvae dominated the distribution (Fig. 6c).

Osmerus mordax — For larval smelt (Table 3), the average increase in size from late May to late June was 4.44 mm (0.15 mm/d) and 3.23 mm (0.10 mm/d) from late June to

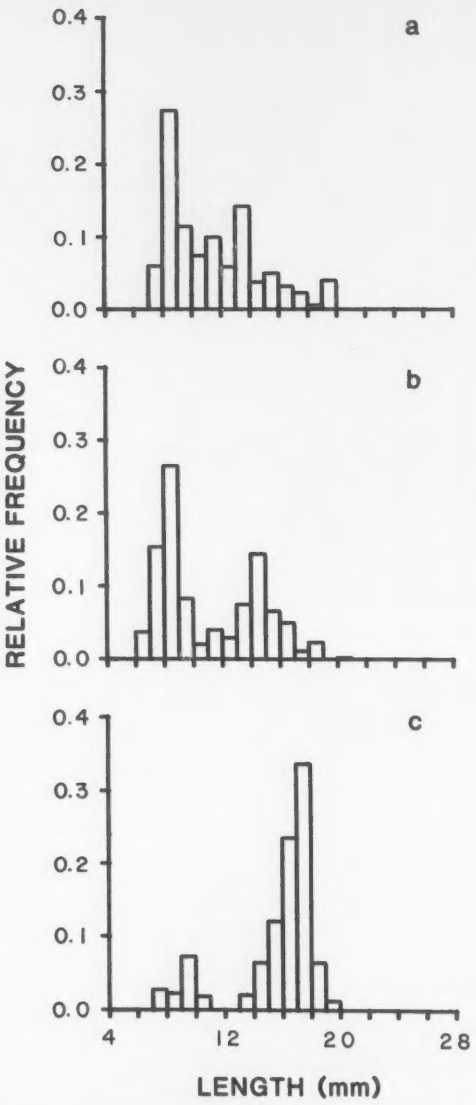

FIG. 6. Size distribution of herring larvae in July: (a) station 79-3, (b) station 79-2, (c) station 79-1.

late July. The entire size distribution regularly shifted to higher values during this period (Fig. 5c).

SMALL-SCALE VARIABILITY

Abundance — At a sampling frequency of 3 h^{-1}, larval densities appeared highly variable and fluctuations over two orders of magnitude were recorded for all species. Coefficients of variation within one time series often exceeded 100% indicating that the larvae were strongly aggregated (Table 4).

Auto- and cross-correlation techniques were used to investigate the short-term variability in larval densities. The application of these techniques requires that the samples are taken at equal intervals in time. In consequence, detailed analysis of short-scale temporal variability was performed on those stations where the time series were uninterrupted (79-2 in June, 79-1 and 79-2 in July).

Mallotus villosus — At station 79-1 in July, variations in capelin abundance were rhythmic and the autocorrelation of the time series revealed a 12-h periodicity (Fig. 7a). The amplitude of the variations in capelin abundance and salinity remained approximately constant over time. The observed gradient was monotonous: larval concentration increased until a maximum was reached at slack water of high tide and then decreased until slack water of low tide (Fig. 8a). The cross correlation against the longitudinal component of current (u) indicated that maximum abundance occurred 3 h before maximum ebb and was therefore associated with the slack water of high tide. Fluctuations in capelin abundance were in phase with variations in salinity (Fig. 8a). At station 79-2 in June, variations in capelin abundance were less regular; the cross correlation suggests that abundance was in phase with longitudinal advection and lagged salinity by 3 h (Fig. 8b). Similar results were obtained at station 79-2 in July.

The correlation between abundance and the lateral component of current (v) was weak but always negative (Table 5). As v is arbitrarily positive in the North−West direction, a negative correlation indicates that higher larval concentrations are associated with water advected from the north shore of the estuary (Fig. 1).

Clupea harengus harengus — Short-term fluctuations in herring abundance were generally related to tidal advection. At station 79-2 in June, variations in the abundance had a tidal character and the autocorrelation revealed a 12-h periodicity (Fig. 7b). The amplitude of fluctuations in abundance of herring larvae and salinity was maintained over time (Fig. 8c). The gradient of herring abundance, like the gradient of capelin abundance, was monotonous. Again, cross correlation with longitudinal advection associated high larval densities to slack water at high tide and indicated that fluctuations in abundance were in phase with salinity. Similar results were obtained at station 79-2 in July, with the exception that the amplitude of the fluctuations in abundance decreased faster than the amplitude of the fluctuations in salinity (Fig. 8d). At station 79-1 in July, herring abundance was not related to longitudinal advection or to salinity.

Like capelin abundance, herring abundance was only weakly correlated to v (Table 5). The correlation, however, was always positive. The lateral gradient of herring concentration was thus positive in the direction of the south shore.

Osmerus mordax — Short-term variations in smelt abundance were always related to salinity (Table 6). The gradient was sometimes in phase with the gradient of salt (positive correlation) and sometimes dephased by 180° (negative correlation). Correlations of similar magnitude but of opposite sign were found between smelt abundance and temperature which is strongly and negatively correlated with salinity in this section of the estuary in the summer (Fortier et al. 1978).

TABLE 4. Coefficient of variation (%) in the short-term fluctuations in larval fish abundance (integrated over the top 60 m) at stations 79-1, 79-2, and 79-3 of the St. Lawrence estuary in May, June, and July, 1979. Values in parentheses represent the sample size.

	Capelin			Herring			Smelt		
	79-1	79-2	79-3	79-1	79-2	79-3	79-1	79-2	79-3
May	129	94	75	—	—	—	122	70	—
	(13)	(4)	(5)	—	—	—	(13)	(4)	—
June	133	127	76	76	105	64	70	111	99
	(13)	(16)	(13)	(13)	(16)	(13)	(13)	(16)	(13)
July	171	100	79[a]	76	79	100[a]	129	400	520[a]
	(16)	(16)	(26)	(16)	(16)	(26)	(16)	(16)	(26)

[a]Calculations based on surface layer (0–20 m) samples.

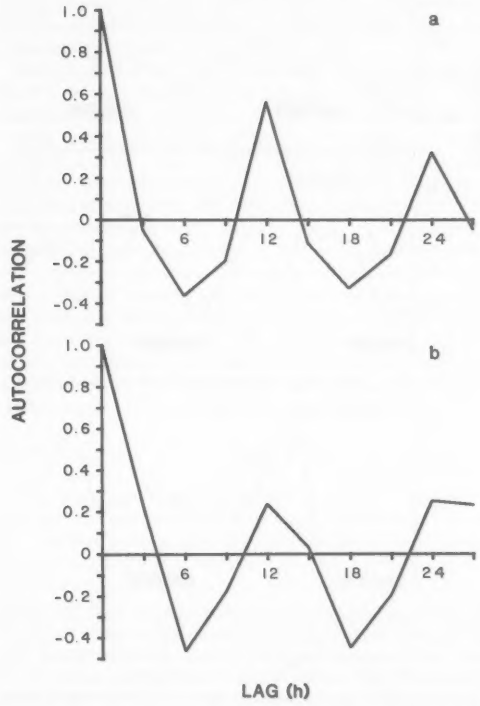

FIG. 7. Autocorrelation on the temporal fluctuations in larval abundance: (a) capelin, station 79-1 in July; (b) herring, station 79-2 in June.

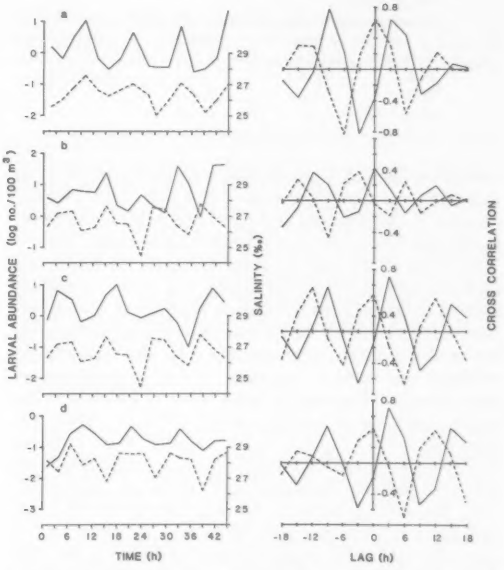

FIG. 8. Fluctuations in larval abundance (—) and salinity (---) (left panel) and corresponding cross correlation between larval abundance and the longitudinal component of current (—) and salinity (---) (right panel): (a) capelin, station 79-1 in July; (b) capelin, station 79-2 in June; (c) herring, station 79-2 in June; (d) herring, station 79-2 in July.

Vertical distribution — The depth of the center of mass (Z_{cm}) was selected as an integrated and simple index of the short-term fluctuations in the vertical distribution of each species.

Mallotus villosus — In June, at station 79-2, the center of mass of the vertical distribution of capelin larvae oscillated between 10 and 32 m (Fig. 9a). These oscillations presented a periodicity of about 12 h (Fig. 10a). Variations in Z_{cm} were negatively correlated ($r = -0.75$, $P < 0.01$) with the Richardson number ($\hat{R}i$), an index of the vertical stability of the water column and positively correlated ($r = 0.71$, $P < 0.01$) to the depth of the 24‰ isohaline, chosen as an indicator of the depth of the pycnocline.

Similar results were obtained at station 79-1 in July. At station 79-2 (July), variations in Z_{cm} were insignificant (coefficient of variation = 3%).

Clupea harengus harengus — In June (station 79-2), the center of mass of herring distribution fluctuated between 32 and 50 m. These fluctuations (Fig. 9b) had a diel character, the larvae exhibiting a positive phototropism. The auto-

TABLE 5. Maximum coefficient of cross correlation (r) between the longitudinal (u) and the lateral (v) components of current speed and larval fish abundance in the St. Lawrence estuary at different stations in June and July, 1979. (* $P < 0.05$.)

	79-2 (June)	79-1 (July)	79-2 (July)
Capelin (u)	0.41	0.64*	0.35
(v)	−0.32	−0.47	−0.22
Herring (u)	0.71*	0.62*	0.74*
(v)	0.30	0.24	0.22

TABLE 6. Correlation between smelt abundance and salinity at stations 79-1, 79-2, and 79-3 of the St. Lawrence estuary in May, June, and July, 1979. (*$P < 0.05$.)

	May	June	July
79-1	0.67*	—	0.66*
79-2	—	−0.54*	—
79-3	—	−0.78*	—

correlation showed a predominant rhythmicity of 24 h but also revealed a superposed peak at 12 h (Fig. 10b). The correlogram is characteristic of a signal composed of diel oscillations and tidal oscillations (Demers and Legendre 1979).

At station 79-2 in July, the center of mass of the distribution oscillated between 15 and 44 m (Fig. 9c). These oscillations brought the bulk of the distribution close to the pycnocline. Larvae captured at this station were separated according to the two modes of their size distribution (Fig. 6b). Both cohorts exhibited diel vertical migrations. These migrations were more pronounced among the larger larvae as indicated by the larger coefficient of variation in Z_{cm} (57% vs. 36%). The correlogram on Z_{cm} for larvae smaller than 11.5 mm (Fig. 10c) is similar to that of larval herring in June (Fig. 10b) with a dominant diel periodicity and a secondary tidal periodicity. The correlogram of Z_{cm} for larvae larger than 11.5 mm indicates a diel periodicity only (Fig. 10d). At station 79-1 in July, only 13% of the larvae were smaller than 11.5 mm. The vertical migrations were more extensive (10−50 m), and the center of mass of the distribution crossed the pycnocline at approximately 08:00 on the two days sampled (Fig. 9d). The autocorrelation (not shown) on Z_{cm} for these larger herring revealed a 24-h cycle only.

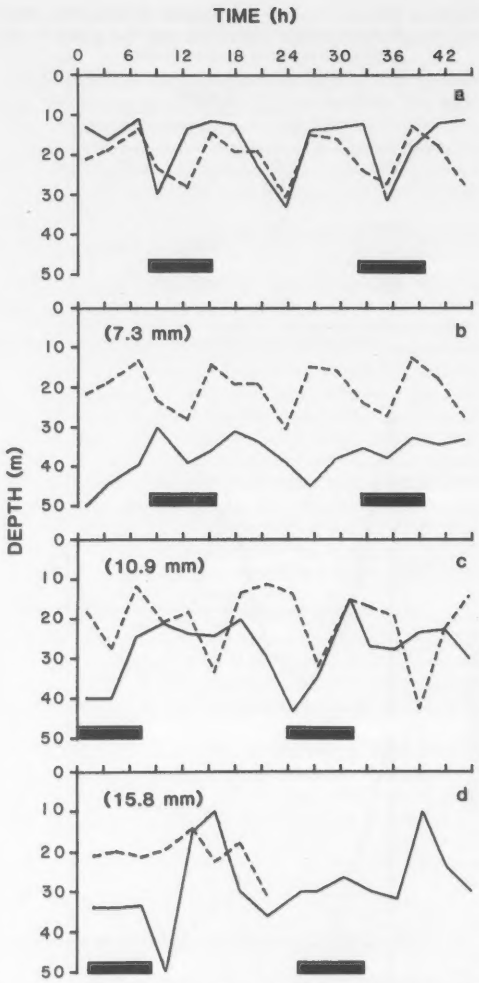

FIG. 9. Fluctuations in the depth of the center of mass (Z_{cm}) of the larval distribution (—) and in the approximative depth of the pycnocline (---): (a) capelin, station 79-2 in June; (b) herring, station 79-2 in June; (c) herring, station 79-2 in July; (d) herring, station 79-1 in July. Heavy horizontal bars indicate darkness. The average standard length of herring larvae is given in parentheses.

Discussion

LARGE-SCALE FLUCTUATIONS IN ABUNDANCE

Persistence of high densities of capelin until the end of June probably reflects the duration of the spawning activities, the subsequent sharp decline in abundance being attributed to the termination of recruitment to the larval population, seaward drift, and mortality (Jacquaz et al. 1977).

The later downstream appearance of herring and the subsequent decrease in number at the seaward stations is consistent with the observations of Able (1978) and probably reflects both mortality and the upstream movement of the center of mass of the larval population reported by this author.

Smelt abundances fall into the range reported by Able (1978) for these months in this area. He reported that the bulk of the distribution is located above Ile aux Coudres. The very low concentrations we encountered downstream of that point would appear to represent the lower limit of their distribution.

In summary, the main characteristics of the seasonal distribution documented in detail by Jacquaz et al. (1977) and Able (1978) also underlie the 1979 results. These characteristics are (a) the numerical dominance of capelin, (b) the seaward flush-

ing of this species, (c) the late appearance and upstream movement of herring, and finally (d) the retention of smelt in the upper reaches of the estuary.

Residual Circulation and Vertical Distribution

The values of residual circulation presented here are purely indicative and can by no means be considered as precise estimates. With a sampling interval of 3 h, maximum ebb and flood are likely to be masked (Meric 1975), and the seaward flow was probably underestimated as values of current above 3 m (where the intensity is maximum) were not available. Yet, the general picture obtained agrees well with the two-layer circulation previously described for the area (d'Anglejan and Smith 1973; Meric 1975). The deep layer was about 3 times thicker than the surface layer but the absolute values of flow were approximately the same in the two layers. From considerations of continuity of volume, the existence on the south shore of a downstream compensatory current must be inferred (Ingram 1979).

Stratification of the water column (Fig. 2) changed in space from a partially mixed condition (station 79-1) to a more stratified situation (station 79-3). The vertical distribution of capelin and small herring larvae (Fig. 3a and b, in June) changed similarly from a well-defined two-layer situation (partially mixed distribution) to a smoother vertical gradient (stratified distribution). The parallelism in the progression of the two phenomena is illustrated in Fig. 4. Thus, on a large longitudinal scale, capelin larvae are vertically mixed along with freshwater while small herring larvae are distributed like salt. Given the nature of the circulation, most capelin larvae will drift out of the upper estuary along with the surface layer, and small herring larvae will be carried landward with the deep layer. This is in agreement with the reported seasonal development of the longitudinal distribution of capelin (Jacquaz et al. 1977) and herring larvae (Able 1978).

Growth

The absence of significant growth in capelin is consistent with the fact that the larvae are continuously removed from the sampling area. In July, the collection at the most downstream station of a few larger larvae was associated with the highest salinities recorded during the entire sampling period. The water mass containing these larger larvae was typical of the lower estuary. This supports the hypothesis that significant growth begins in this area only (Jacquaz et al. 1977).

The average growth rate of herring larvae from the end of June to the end of July was 0.15 mm/d. Able (1978) reported values of 0.15 mm/d from June to October 1974 and 0.17 mm/d from June to September, 1975. If the second mode of the size distribution in July and the single mode found in June (Fig. 5b) pertain to the same cohort, then the calculated growth rate increases to 0.27 mm/d. This value is still much lower than the value of 0.5 mm/d reported by Ware and Henriksen (1978) for the spring herring of the Magdalene Islands. Côté et al. (1980) related the smaller size of adult herring in the St. Lawrence estuary to these low rates of larval growth.

The numerical dominance of small larvae at the downstream station and the progressive reversal of this situation from downstream to upstream (Fig. 6) is in agreement with a landward transportation of herring larvae from the spawning grounds located in the area of Ile Verte (Fig. 1).

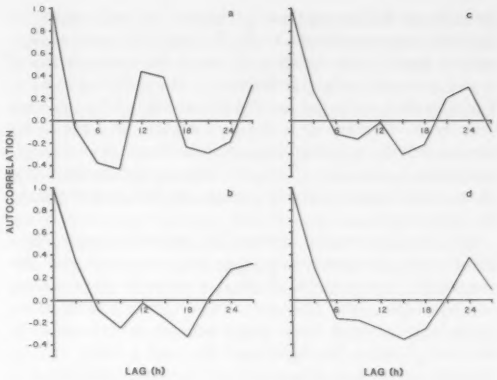

FIG. 10. Autocorrelation on the temporal fluctuations in Z_{vm}: (a) capelin, station 79-2 in June; (b) herring, station 79-2 in June; (c) herring (<11.5 mm), station 79-2 in July; (d) herring (>11.5 mm), station 79-2 in July.

From the end of May to the end of July, the average growth rate of smelt larvae was 0.13 mm/d. Able (1978) reported a value of 0.24 mm/d for the population located in the area of Ile aux Coudres. As the area sampled represents the downstream limit of larval smelt distribution, the lower value obtained in this study may reflect suboptimal conditions of growth for this species.

Larval Dispersal

After emergence, larval dispersal (i.e. the change in the extent and location of the spatial distribution) will depend both on net advection and diffusion. Displacement of the larvae due to the displacement of the volume of water in which they occur is called advection. Any process by which a particle moves from one volume of water into another is called a diffusive process. For example, salt can move into freshwater by molecular diffusion or turbulent diffusion. Molecular diffusion is a very weak process and obviously does not act on larval fish. Given their size, larvae are subject to turbulent diffusion. Active swimming is a supplementary mechanism by which larval fish can diffuse.

In a partially mixed estuary, longitudinal and lateral diffusion are relatively weak processes compared to longitudinal and lateral advection. Vertical diffusion, however, cannot be neglected given the smaller scale of the vertical axis (Pritchard 1955). Thus, the Fickian representation of transport for a conservative and passive contaminant of the water can be reduced to four terms:

$$(1)\quad \frac{\delta c}{\delta t} = \frac{u\delta c}{\delta x} + \frac{v\delta c}{\delta y} + \frac{w\delta c}{\delta z} - \frac{\delta}{\delta z}\left(K_z \frac{\delta c}{\delta z}\right)$$

where $\delta c/\delta t$ is the change in concentration of contaminant c over time at a fixed location; u, v, and w are the current

velocities in the longitudinal (x), lateral (y), and vertical (z) direction, respectively; $\delta c/\delta x$, $\delta c/\delta y$, and $\delta c/\delta z$ are the longitudinal, lateral, and vertical gradients in the concentration of c; and finally K_z is the coefficient of vertical diffusivity of c. The first three terms on the right-hand side of the equation describe the fluctuations in the concentration of c due to the advection at the sampling location of the longitudinal, lateral, and vertical gradient of c. The last term represents the fluctuations in the concentration of c due to the diffusion of c along the vertical axis.

On a long-term basis, larval fish cannot be equated to a conservative contaminant because they disappear from the environment by predation or decay after death. On the scale of a few tidal cycles, however, the contribution of mortality to the fluctuations in larval abundance can be assumed to be minimal. Indeed, no significant decreasing trend can be detected in the four time series of abundance presented in Fig. 7 and, hence, the larvae can be considered as roughly conservative over these 48-h periods. It is therefore possible to test if the ichthyoplankton is dispersed passively by verifying that the fluctuations in larval abundance ($\delta L/\delta t$) at a given sampling station are controlled by the same processes (eq. 1) that control the fluctuations of a passive contaminant.

Horizontal dispersal — When larval densities are integrated over depth (as in Fig. 8), the observed fluctuations in abundance represent the effect of horizontal transport.

Diffusion — The amplitude of the fluctuations in the abundance of capelin larvae and herring larvae smaller than 10 mm remained approximately constant from one tidal cycle to the next (Fig. 8a and c). This persistence indicates that the dampening of the horizontal gradient by diffusion is slow. As the gradient of larval abundance was not dissipated faster than the gradient of salinity, it can be concluded that the increase in horizontal diffusivity due to active swimming is small. Thus, short-term variations in the abundance of capelin and small (<10 mm) herring larvae, in the horizontal plane, are due primarily to the advection of a horizontal gradient. This agrees with the observations of Gagnon and Lacroix (1981) on estuarine zooplankton variability. The terms of longitudinal and lateral diffusion appear relatively unimportant. Talbot (1977, 1978) reached a similar conclusion following a study of the dispersal of plaice (*Pleuronectes platessa*) larvae in the Southern Bight of the North Sea. Herring larvae captured in July appeared to diffuse faster than salt in the horizontal plane. This phenomenon is discussed in the section on vertical diffusion.

Advection — Temporal variations in larval abundance caused by the advection of a horizontal gradient ($\delta L(\mathrm{h})/\delta t$) can be decomposed into a longitudinal and a lateral component:

$$\frac{\delta L(\mathrm{h})}{\delta t} = \frac{u\delta L}{\delta x} + \frac{v\delta L}{\delta y}$$

where $\delta L/\delta x$ and $\delta L/\delta y$ are, respectively, the longitudinal and lateral gradients of larval abundance. Cross-correlation analysis showed that total fluctuations in capelin and herring abundance are more strongly correlated to the longitudinal component of advection (u) than to the lateral component (v). Thus, the advection of the longitudinal gradient of larval concentration [$u(\delta L/\delta x)$] explained a larger proportion of the observed variability than the advection of the lateral gradient [$v(\delta L/\delta y)$] (Table 5).

In general, longitudinal gradients were monotonous and in phase with the gradient of salinity. The formation and orientation of these gradients are possibly linked to the mechanism of emergence (Fortier and Leggett unpublished data). Lateral gradients of capelin abundance were positive toward the north shore where the closest spawning grounds are located (Parent and Brunel 1976). Lateral gradients of herring abundance were positive toward the south shore, the principal location of spawning areas for this species in the estuary (Tremblay 1942).

Vertical dispersal — Day–night differences in catchability can mask real fluctuations in the vertical distribution of the larvae. On average, night densities of capelin and herring larvae were not significantly larger than day densities, suggesting that sampler avoidance was not important. Jacquaz et al. (1977), also using a bongo sampler, reached the same conclusion for capelin larvae. This relatively low avoidance of the nets can be explained by the high turbidity of the water as suggested by Weinstein et al. (1980). Secchi disk readings never exceeded 2 m in the sampling area. It has been suggested (Isaacs 1964) that, among the larger larvae, only the weakest, starving individuals are captured in net collections. This might be especially true for large herring larvae (10–15 mm) captured in July. However, high incidence of feeding in this month (30.5%: Courtois and Dodson unpublished data) discredits the possibility of such a bias in the present study.

Advection — The vertical component of advection (w) cannot be calculated from the available data. However, typical values of vertical velocity in estuaries are in the order of 10^{-3} cm/s (3.6 cm/h) (Dyers 1973, p. 31) and cannot account for the observed short-term variations of several tens of metres in Z_{cm} for capelin and herring.

Diffusion — The negative correlation between the depth of the center of mass of capelin distribution and the Richardson number suggests that capelin larvae do not resist the vertical turbulent mixing induced by tidal currents. On the other hand, fluctuations in Z_{cm} are also correlated to the variations in the depth of the pycnocline. If the larvae are concentrated at the bottom of the surface layer, then the tidal fluctuations in the level of the pycnocline could explain the observed 12-h cycle in the fluctuations of Z_{cm}. To assess the relative importance of vertical turbulent mixing and variations in the depth of the pycnocline, the short-term fluctuations, in June, of the vertical distribution of capelin larvae and the corresponding fluctuations in the depth of the isopycnals are presented together in Fig. 11. Capelin larvae were generally concentrated within the first 20 m of the water column. The only exceptions to this pattern occurred at the end of ebb when the potential instability of the water column is maximum (Fortier and Legendre 1979). At that time, the vertical distribution of larval capelin became uniform and significant numbers of larvae were captured below the pycnocline in the 20- to 40-m and the 40- to 60-m strata. Thus, the larvae were actually mixed through the pycnocline approximately at the time when vertical turbulent mixing is expected to be maximum.

The lack of simultaneity between the measurement of the physical parameters and the measurement of the vertical dis-

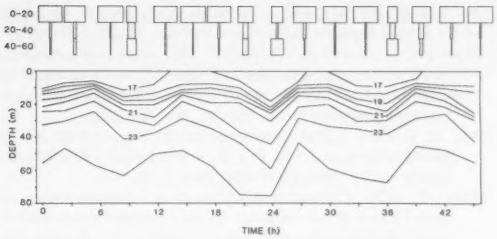

FIG. 11. Short-term fluctuations in the vertical distribution of capelin larvae at station 79-2 in June (histograms) and corresponding fluctuations in the depth of the isopycnals (σ_t).

tribution, and the rather large temporal (3 h) and vertical (20 m) sampling intervals complicate the identification of the dominant factor in the control of the fluctuations in Z_{cm}. Higher sampling frequency and longer time series of simultaneous measurements are needed to confirm the role of vertical turbulent mixing. Our results do, however, strongly suggest that capelin larvae are mixed through the pycnocline by the same tidal processes that mix freshwater. This hypothesis is supported by the similar large-scale variation of the vertical distribution of capelin larvae and freshwater (Fig. 4). There is no indication that this species performed active diel migrations across the density boundary between the two layers.

Vertical displacement of herring larvae resulted from a combination of active diel migrations and tidal mixing. The influence of tidal mixing apparently decreased as body length increased (Fig. 10b, c, and d). In contrast, the amplitude of diel migrations increased with size. This last relation has been noted previously for herring (Wood 1971; Selivertov 1974), haddock (*Melanogrammus aeglefinus*) (Miller et al. 1963), and yellowtail flounder (*Limanda ferruginea*) larvae (Smith et al. 1978).

Talbot (1977, 1978) found that the interaction between vertical diffusion and the vertical gradient of current speed was the most important factor of diffusion for plaice eggs and larvae in the Southern Bight of the North Sea. The vertical diffusivity of larvae performing extensive vertical migrations will be greater than the vertical diffusivity of a passive contaminant like salt. This added vertical diffusivity, interacting with the strong vertical gradient of current speed found in the upper estuary of the St. Lawrence, should produce a faster rate of horizontal diffusion than the one expected for a passive contaminant. Vertical migrations of herring larvae captured in June (average standard length = 7.3 mm) were limited to the deep layer (Fig. 9b), and little interaction could take place with the bulk of current shear located at the interface between the surface layer and the deep layer. As previously noted, herring larvae captured in June did not diffuse faster than salt in the horizontal plane. Herring larvae captured at station 79-2 in July (average standard length = 10.8 mm) performed diel migrations that brought the center of mass of the distribution close to the pycnocline (Fig. 9c). The resulting interaction with the current shear apparently increased the rate of horizontal diffusion, and the horizontal gradient of larval abundance was dampened faster than the salt gradient. At station 79-1 in July, the diel vertical migrations of herring larvae (average standard length = 15.8 mm) were extensive (Fig. 9d), and the interaction with the vertical gradient of current speed produced a highly variable horizontal distribution that bore no relation to the gradient of salt. Such a result is predicted by numerical models of the interaction between diel vertical migrations of planktonic animals and tidal current shear (Kamykowski 1976; Evans et al. 1977).

Smith et al. (1978) emphasized the importance of investigating the diel movements of larval fish before hypothesizing on how circulation affects their distribution and survival. In the St. Lawrence estuary, short-term vertical movements of capelin larvae were passive and controlled by tidal processes. The absence of active migrations across the pycnocline prevented the larvae from diffusing faster than freshwater in the horizontal plane. Thus, on the scale of a few tidal cycles, the terms of the Fickian equation of transport in partially mixed estuaries are sufficient to describe the fluctuations in capelin abundance, and the dispersal of larvae smaller than 7 mm is passive. This passivity is reflected at larger scales by the seaward transition from a two-layer (partially mixed) vertical distribution to a smoother (stratified) vertical gradient. Jacquaz et al. (1977) found no indication of diel vertical migrations for capelin larvae up to 40 mm and laboratory studies (Rosenthal and Hempel 1970; Hunter 1972) showed that swimming activities of larval fish do not increase significantly until active feeding begins. Therefore, capelin larvae can be expected to disperse passively at least until the transition from yolk sac to exogenous feeding.

Vertical migrations of herring larvae increased with size. In a two-layer circulation, these diel migrations have little effect on the horizontal dispersal of the larvae as long as they are limited to one layer. Like capelin larvae, herring larvae smaller than 10 mm did not actively cross the pycnocline and their dispersal paralleled the dispersal of salt with the persistence of horizontal gradients and the seaward transition from a partially mixed to a stratified vertical distribution. The amplitude of the vertical migrations and thereby the horizontal diffusivity of herring larvae larger than 10 mm increased with body size until extensive migrations across the pycnocline produced a complicated pattern of horizontal distribution. Thus the divergence between the dispersion of herring larvae and the dispersion of salt increased with body length for larvae larger than 10 mm which cannot be considered as passive contaminant of the environment.

While the results presented in this paper represent a first approach, and longer time series of higher frequency sampling are needed to confirm our conclusions, they do suggest that a Fickian representation can be profitably applied to the study of dispersal and mortality of early fish and invertebrate larvae in estuaries.

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Interactions multispécifiques : répartition spatio-temporelle des larves de capelan (*Mallotus villosus*), d'éperlan (*Osmerus mordax*) et de hareng de l'Atlantique (*Clupea harengus harengus*) au sein de la communauté planctonique de l'estuaire moyen du Saint-Laurent[1]

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L'étude de l'organisation spatio-temporelle de la communauté planctonique de l'estuaire moyen du Saint-Laurent démontre que le mode de répartition des larves de poisson dans le milieu tend à minimiser les interactions entre espèces. Les larves d'éperlan (*Osmerus mordax*) plus représentatives des masses d'eau d'amont se séparent des larves de capelan (*Mallotus villosus*) et de hareng de l'Atlantique (*Clupea harengus harengus*) plus typiques des masses d'eau d'aval au mois de juin. De plus, les larves de capelan sont plus abondantes en surface (0–20 m), alors que les larves de hareng sont concentrées dans les couches plus profondes (20–60 m). La séparation écologique observée, maintenue par les processus physiques du milieu, semble être la conséquence de stratégies de reproduction différentes. En ce qui a trait aux interactions zooplancton–ichtyoplancton l'abondance des chaetognathes, des amphipodes et des euphausiacés en profondeur rend possible la prédation des larves de poisson par ces grosses formes zooplanctoniques. Les larves de capelan, très nombreuses en juin, peuvent être l'objet de prédation par les organismes du macroplancton lors de leurs migrations nycthémérales. Les larves de hareng sont également vulnérables en raison de leur plus grande abondance en profondeur. Les larves d'éperlan risquent toutefois moins d'être touchées par cette prédation à cause de leur prépondérance en amont dans les eaux plus douces.

Mots clefs: ichtyoplancton, interactions multispécifiques, communauté planctonique, estuaire du Saint-Laurent, capelan, hareng, éperlan

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The study of the spatial and temporal organization of the planktonic community of the middle estuary of the Saint Lawrence River revealed that fish larvae were distributed in such a way as to minimize interactions between species. Smelt (*Osmerus mordax*) larvae were distributed upstream whereas capelin (*Mallotus villosus*) and Atlantic herring (*Clupea harengus harengus*) larvae were found downstream in June 1979. Capelin larvae were more abundant at the surface (0–20 m) whereas herring larvae were concentrated in deeper waters (20–60 m). The ecological separation observed was maintained by multiple physical factors and appeared to be the consequence of species-specific reproductive strategies. The abundance of chaetognaths, euphausiids, and amphipods in deeper waters suggests that these forms could be important predators of fish larvae. Herring larvae may be particularly vulnerable because of their distribution in deep water. Capelin larvae which are very abundant in June could also be vulnerable to predation during the diurnal migrations of the macroplankton. Smelt larvae appear to be little affected by predation from these forms as a result of their distribution in fresher waters.

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On considère généralement que le régulateur du recrutement et de l'abondance des poissons est surtout une combinaison de la croissance et de la mortalité due à la densité qui se produit chez les stades très jeunes (Cushing 1974; Ware 1975). Les hypothèses quant aux causes de la mortalité larvaire sont nombreuses. Lett et Kohler (1976) en donnent un résumé et rappellent notamment l'importance de la nourriture disponible. De plus, Lett et Kohler (1976) discutent les implications des relations multispécifiques, domaine déjà abordé par Isaacs (1963). Finalement, Hunter (1976) ajoute que la prédation doit être considérée comme un facteur de première importance, car elle implique autant des poissons (Lett et Kohler 1976; Sinderman 1979) que divers groupes zooplanctoniques tels les chaetognathes (Lebour 1923; Fraser 1969; Williams et Hart 1974), les amphipodes (Westernhagen et Rosenthal 1976; Sheader et Evans 1975), et les euphausiacés (Theilacker et Lasker 1974). L'étude des relations unissant les différents groupes taxonomiques de la communauté planctonique devient donc nécessaire pour une meilleure compréhension des causes de mortalité au sein de l'ichtyoplancton. Aucune étude quantitative n'existe toutefois pour déterminer l'influence des interactions multispécifiques sur la mortalité des larves de poisson en milieu naturel.

L'estuaire moyen du Saint-Laurent est un site de frai et/ou d'alevinage pour certaines espèces de poisson d'importance commerciale. Ainsi, Jacquaz et al. (1977) mentionnent la mise en circulation massive des larves de capelan (*Mallotus villosus*) en mai et, malgré la pauvreté du milieu rapportée par Bousfield et al. (1975), Able (1978) soutient que l'estuaire moyen du Saint-Laurent sert de site d'alevinage pour l'éperlan (*Osmerus mordax*) et le hareng de l'Atlantique (*Clupea harengus harengus*). Les larves de ces trois espèces, pélagiques et semblables morphologiquement, se trouvent dans la même région de l'estuaire en juin et pourraient alors entrer en compétition. De plus, il existe au sein de la communauté planctonique certaines formes telles les chaetognathes, les euphausiacés et les amphipodes qui pourraient être prédatrices des larves de ces trois espèces de poisson.

Le présent travail vise à décrire l'organisation spatio-temporelle d'une communauté planctonique, et à mettre en évidence les chevauchements de répartition des larves de capelan, d'éperlan et de hareng de même que leurs relations avec les taxons zooplanctoniques. Ainsi, les possibilités d'interactions multispécifiques telles la compétition entre les larves pour les ressources disponibles et la prédation par le zooplancton sur ces mêmes larves sont évaluées. À cette fin, les groupes d'espèces réagissant de la même façon aux caractéristiques de leur milieu (Fager et McGowan 1963) sont identifiés, et les tendances générales de la variabilité observée dans la distribution et l'abondance de ces groupes, à moyenne et à petite échelle, sont décrites.

Matériel et méthodes

L'échantillonnage fut réalisé à trois stations de l'estuaire moyen du Saint-Laurent (Fig. 1) distantes l'une de l'autre de quelque 25 km. En 1979, les trois stations ont été échantillonnées dans leur ordre numérique en mai, juin et juillet. Le présent travail ne traite toutefois que des 129 échantillons recueillis en juin, période où se trouvent ensembles les

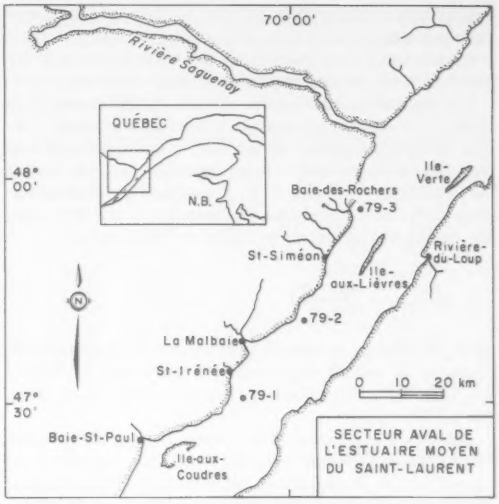

FIG. 1. Secteur aval de l'estuaire moyen du Saint-Laurent, indiquant la position des stations d'échantillonnage en 1979 (79-1: 47°30,8'N, 70°10,8'W; 79-2: 47°42,4'N, 69°57,0'W; 79-3: 47°57,7'N, 69°45,0'W).

larves des trois espèces étudiées telle que révélée par une analyse préliminaire. À chaque station, la colonne d'eau fut divisée en trois couches (0–20 m, 20–40 m et 40–60 m), afin d'étudier la répartition verticale des larves. Un prélèvement oblique multiple d'une durée de 10 min a été effectuée dans chaque strate, à toutes les 3 h, pendant 48 h. L'échantillonnage a pris place en période de vive-eau et a été complété en 8 jours.

Les échantillons ont été prélevés au moyen d'un échantillonneur Bongo de 0,5 m de diamètre (McGowan et Brown 1966), muni de débitmètres, et de filets de mailles n° 0 (0,51 mm) et n° 10 (0,15 mm). Des difficultés mécaniques nous ont forcé à utiliser l'échantillonneur sans son mécanisme d'ouverture. La descente du filet en position ouverte a probablement eu pour effet de contaminer les échantillons des couches profondes, contamination cependant minime, la filtration étant sans doute moins efficace lors d'une descente rapide de l'engin de pêche. De plus, le temps de contamination ne constituait qu'environ 5% de la durée du prélèvement puisque les filets étaient fermés lors de la remontée.

Les traits ont été effectués à une vitesse de deux à trois nœuds. La profondeur des traits a été lue de façon continue grâce à un profondimètre Furuno et a été vérifiée avec un bathychronographe (*TDR*, *Time depth recorder*) placé sur le câble entre le profondimètre et le dépresseur. Avant chaque série de traits, le navire était ancré à une bouée indiquant l'emplacement de la station. La température, la conductivité, la vitesse et la direction des courants étaient alors enregistrées à intervalles de 0,5 min au moyen d'un courantomètre Aanderaa muni de senseurs STP (salinité–température–pression) lors d'un profilage de la colonne d'eau par palier de 5 m. Ces valeurs ont servi à calculer la salinité et la densité des masses d'eau échantillonnées. La vitesse et la direction

des courants sont exprimées par deux vecteurs, soit la composante u correspondant à l'axe de l'estuaire et la composante v correspondant à l'axe transversal. La valeur moyenne de ces variables a été calculée pour chaque strate de 20 m.

Les paramètres additionnels suivants ont été ajoutés à la matrice des données physiques: l'heure du prélèvement, l'indice de turbidité (disque de Secchi), la température de surface, l'éclairement (nuit = 0, pénombre (04:00 à 06:00 et de 20:30 à 22:30) = 1, jour = 2), l'amplitude de la marée calculée pour l'heure de chaque prélèvement à partir de la table des marées et finalement, un indice de stratification:

$$\Delta\sigma_{t\,5-35} = \frac{\sigma_{t_p} - \sigma_{t_s}}{\Delta Z}$$

où σ_{t_p} représente la densité enregistrée à la profondeur de 35 m, σ_{t_s}, la densité enregistrée à la profondeur de 5 m, et ΔZ, l'intervalle de profondeur entre les niveaux où σ_{t_p} et σ_{t_s} ont été mesurées.

Tous les échantillons ont été conservés dans une solution tamponnée de formaline 4%. Au laboratoire, les gros organismes tels les chaetognathes, les mysidacés, les euphausiacés et les amphipodes furent retirés de chacun des échantillons identifiés et comptés. Le reste de l'échantillon fut fractionné un certain nombre de fois à l'aide d'un partiteur Folsom, et une fraction utilisée pour le dénombrement et l'identification des autres groupes (ou espèces). Dans le cas où le dénombrement réalisé pour un groupe (ou une espèce) donnait un nombre inférieur à 200, l'échantillon était trié dans sa totalité afin d'obtenir le nombre total d'individus de ce groupe (ou espèce). Les larves de poisson furent identifiées à l'espèce pour le capelan, l'éperlan et le hareng; les autres larves étant regroupé sous l'étiquette Pisces. Le reste du zooplancton fut divisé en grands groupes taxonomiques. Les copépodes (>2 mm) furent séparés des formes plus petites regroupées sous l'appellation microplancton (≤2 mm). Cette classification sommaire des organismes zooplanctoniques pour les fins de l'étude, déjà utilisée par d'autres auteurs dont Lasker (1975), semble appropriée puisque la taille des proies est généralement plus limitative que l'espèce pour les larves de poisson (Jones et Hall 1974). Les valeurs d'abondance enregistrées ont par la suite été ramenées en nombre d'individus par 100 m^3.

Les densités d'organismes évaluées par les deux types de filet ont été comparés par niveau (0−20 m, 20−40 m et 40−60 m) à l'aide d'un test chi-carré lorsque la distribution ne s'éloignait pas significativement ($P < 0{,}05$) d'une distribution normale; en absence de normalité, le test non-paramétrique de Wilcoxon pour données pairées a été utilisé. Lorsque les deux distributions ne différaient pas de façon significative entre elles, la moyenne des deux échantillons (filets n° 0 et 10) fut utilisée comme meilleur estimateur de la densité d'un taxon donné. Dans le cas contraire, la valeur obtenue par le filet donnant la plus grande densité a été considérée pour les calculs subséquents.

Les données obtenues ont été traitées à l'aide d'une analyse en composantes principales car cette méthode permet d'étudier à la fois les relations entre descripteurs (taxons) aussi bien que les liens entre objets (échantillons). Des explications détaillées de cette méthode sont disponibles dans Laforge (1981) et Legendre et Legendre (1979).

La présente étude a été menée à partir de matrices de corrélations pour donner un poids équivalent à chaque descripteur. Ces matrices sont calculées à partir des données normalisées par transformation logarithmique pour une utilisation optimale de la méthode (Legendre et Legendre 1979). Comme la présence d'un trop grand nombre de doubles zéros peut fausser la valeur des corrélations (Ibanez 1972), ce type d'analyse doit être effectuée sur les espèces présentes dans plus de 30% des échantillons (Legendre et Simard 1979). Dans la présente étude, tous les taxons recensés répondent à ce critère, l'éperlan étant le moins fréquent avec 47,9% d'occurrence.

La nature des axes d'ordination est déterminée par des corrélations non paramétriques (τ de Kendall) entre les composantes principales et les paramètres physiques du milieu. Les corrélations non-paramétriques sont utilisées puisqu'elles n'exigent ni la normalité ni la linéarité (Legendre et Simard 1979). Des corrélations partielles sont calculées lorsque plusieurs descripteurs sont liés entre eux afin de connaître la contribution unique des descripteurs aux axes d'ordination.

Dans la première partie de l'étude, les trois stations de juin sont traitées simultanément et les échantillons font l'objet d'un groupement a priori par station. Dans la seconde partie où la station de plus grande variabilité est traitée (station médiane 79-2), les échantillons sont soumis à un groupement à liens complets à partir de la matrice de leurs distances euclidiennes calculées sur les données normalisées et centrées réduites (Legendre et Legendre 1979; Legendre et Simard 1979). L'échantillonnage ayant été réalisé dans un continuum, le groupement à liens complets permet de dégager la structure de façon plus contrastante (Legendre et Legendre 1979). Ce groupement des échantillons est par la suite superposé à leur ordination dans le plan réduit des premiers axes principaux ce qui permet de délimiter les groupes d'échantillons semblables par leur composition planctonique et de visualiser les relations entre ces groupes.

Résultats

La communauté planctonique

Dans la présente étude, les organismes planctoniques sont classés selon 15 groupes majeurs. Les larves de poisson sont représentées par trois espèces: le capelan (*Mallotus villosus*), l'éperlan (*Osmerus mordax*) et le hareng de l'Atlantique (*Clupea harengus harengus*), les larves des autres espèces de poisson étant regroupée sous le terme, Pisces. Le reste du zooplancton comprend 10 groupes: deux genres d'euphausiacés (*Meganyctiphanes norvegica* et *Thysanoessa* sp.), un genre de mysidacés (*Mysis* sp.) divisé en deux groupes (juvéniles et adultes), les copépodes (>2 mm), le microplancton (≤2 mm), les amphipodes, les chaetognathes (*Sagitta elegans*), les polychètes errants et les larves de décapodes. Le dernier groupe recensé est constitué des œufs de poisson (Pisces).

À une station donnée, l'abondance relative de chaque groupe reste assez constante malgré les fluctuations de biomasse associées aux marées, ce qui rend les groupes interprétables à cette échelle. Cependant, les abondances relatives

TABLEAU 1. Abondance des organismes zooplanctoniques recensés aux trois stations de l'estuaire moyen du Saint-Laurent en juin, 1979. $\bar{x}$, nombre moyen par 100 m^3; s, écart-type; r, rang occupé par le groupe (ou l'espèce) lorsque les organismes sont ordonnés par ordre décroissant d'abondance à chaque station.

Groupe	Station 79-1			79-2			79-3		
	$\bar{x}$	s	r	$\bar{x}$	s	r	$\bar{x}$	s	r
Mallotus villosus	170,26	374,15	4	494,61	1176,38	3	689,87	948,22	2
Osmerus mordax	1,83	1,70	10	0,14	0,20	15	0,17	0,24	15
Clupea harengus harengus	0,42	0,50	13	11,17	16,94	9	11,82	8,97	5
Pisces (larves)	0,24	0,29	15	0,58	1,02	14	7,83	4,64	7
Meganictiphanes norvegica	16,92	15,29	6	84,09	101,85	5	0,22	0,29	14
Thysanoessa sp.	11,53	7,82	7	47,97	41,39	6	0,49	0,93	11
Mysidacés (adultes)	9,98	9,22	8	24,89	40,74	7	4,81	12,91	8
Mysidacés (juvéniles)	1536,30	1376,05	3	301,13	538,23	4	9,87	34,01	6
Copépodes (> 2 mm)	4437,97	2620,50	2	9445,15	10148,80	2	357,29	329,27	3
Microplancton (< 2 mm)	24525,12	15711,85	1	24537,31	23326,20	1	11499,93	7902,00	1
Sagitta elegans	6,94	5,53	9	6,84	6,49	10	0,20	0,27	13
Amphipodes	1,14	1,12	11	1,28	1,89	13	0,21	0,30	12
Polychètes errants	20,72	17,43	5	4,24	9,1	12	1,65	2,14	10
Décapodes (larves)	0,35	0,42	14	15,35	14,90	8	24,22	13,76	4
Pisces (œufs)	1,05	2,42	12	4,73	8,43	11	1,92	1,50	9

TABLEAU 2. Abondance des organismes zooplanctoniques recensés aux trois couches (0–20 m, 20–40 m, 40–60 m) de la station 79-2 de l'estuaire moyen du Saint-Laurent en juin 1979. $\bar{x}$, nombre moyen par 100 m^3, s, écart-type.

Groupe	0–20 m		20–40 m		40–60 m	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
Mallotus villosus	1285,64	1816,52	99,79	117,92	98,40	146,04
Osmerus mordax	0,23	0,24	0,10	0,14	0,09	0,20
Clupea harengus harengus	3,88	4,15	15,69	23,61	13,93	15,42
Pisces (larves)	0,91	1,48	0,61	0,89	0,23	0,25
Meganictiphanes norvegica	22,73	24,10	117,16	102,72	112,38	113,72
Thysanoessa sp.	18,00	54,62	67,14	41,19	58,78	40,19
Mysidacés (adultes)	11,69	26,07	21,66	20,88	41,33	60,00
Mysidacés (juvéniles)	264,46	581,84	263,94	338,10	374,98	667,93
Copépodes	3182,73	4049,50	11382,64	11422,35	13770,07	10491,46
Microplancton	24781,27	22202,68	28781,93	30663,53	20048,70	15195,40
Sagitta elegans	2,09	1,82	11,79	7,74	6,64	4,31
Amphipodes	0,08	0,23	1,59	2,43	2,17	1,65
Polychètes errants	1,13	2,14	3,89	4,45	7,70	14,56
Décapodes (larves)	8,68	11,09	26,17	15,61	11,90	12,27
Pisces (œufs)	1,34	3,32	5,74	10,12	7,25	9,53

changent d'une station à l'autre (Tableau 1), et à l'intérieur d'une station, d'une couche à l'autre (Tableau 2).

Suite à l'examen de 18 échantillons (soit deux par niveau à chaque strate échantillonnée pour chaque station), il appert que le genre *Calanus* constitue 91,6% des copépodes >2 mm, les genres *Euchaeta* et *Metridia* ne comptant que pour 5,3% et 3,1% respectivement. Par contre, le microplancton s'avère beaucoup plus hétérogène: représenté majoritairement par le genre *Acartia* (46,1%), d'autres taxons composent toutefois une partie importante du microplancton. Ce sont les larves de cirripèdes (19,8%), et le genre *Eurytemora* (9,4%) auxquels se greffent plusieurs autres groupes faiblement représentés dont *Microcalanus*, *Pseudocalanus* et *Scolecithricella*, composant 21,7% du microplancton.

De plus, l'abondance relative des espèces constituant le microplancton change d'une station à l'autre. Ainsi, le genre *Eurytemora* représente 27,3% du microplancton à la station 79-1 mais seulement 0,3% et 0,6% aux stations 79-2 et 79-3. De même, les larves de cirripèdes passent de 6,6% à 11,8% puis à 41,0% du microplancton aux stations amont (79-1), médiane (79-2) et aval (79-3).

ORGANISATION SPATIALE À L'ÉCHELLE DE L'ESTUAIRE MOYEN

L'analyse en composantes principales réalisée à partir de la matrice des corrélations entre groupes produit quatre composantes principales de valeur propre supérieure à 1. Toutefois, seules les composantes I et II sont interprétables puisque la fraction de la variance expliquée par les axes consécutifs est inférieure à celle prédite par le modèle aléatoire de Frontier (1976). Le plan réduit formé par les deux premiers axes prin-

TABLEAU 3. Matrice des corrélations taxons-composantes principales. Les valeurs propres, les pourcentages de variance et le pourcentage de variance cumulé sont indiqués au bas du tableau pour chaque axe. Pour chaque taxon, le carré de la valeur de la corrélation indique le pourcentage de variance expliqué par un axe donné. Les corrélations négatives indiquent une relation inverse avec l'axe d'ordination.

	Stations 79-1, 79-2, 79-3		Station 79-2	
Groupes	Axe I	Axe II	Axe I	Axe II
Mallotus villosus	−0,592	0,077	−0,640	−0,230
Osmerus mordax	0,435	−0,667	−0,255	−0,635
Clupea harengus harengus	−0,460	0,723	0,226	0,848
Pisces (larves)	−0,841	0,075	−0,404	0,652
Meganyctiphanes norvegica	0,820	0,422	0,871	−0,178
Thysanoessa sp.	0,814	0,416	0,860	−0,187
Mysidacés (adultes)	0,677	0,201	0,613	0,074
Mysidacés (juvéniles)	0,851	−0,159	0,544	0,059
Copépodes (≥ 2 mm)	0,846	0,294	0,843	−0,174
Microplancton (< 2 mm)	0,242	0,197	0,078	0,487
Sagitta elegans	0,841	0,227	0,810	−0,077
Amphipodes	0,662	0,248	0,749	−0,104
Polychètes errants	0,575	−0,316	0,494	0,014
Décapodes (larves)	−0,594	0,628	0,365	0,075
Pisces (œufs)	−0,089	0,573	0,337	0,640
Valeurs propres	6,586	2,455	5,285	2,375
Variance expliquée (%)	43,9	16,4	35,2	15,8
Variance cumulée (%)	43,9	60,3	35,2	51,1

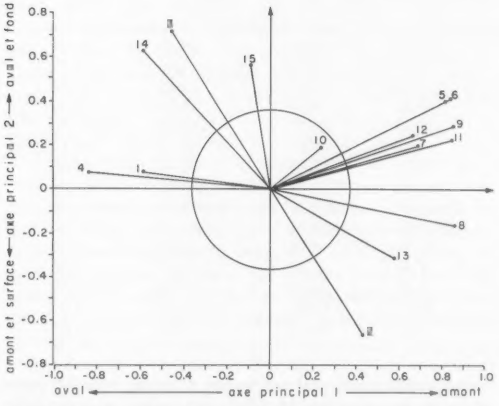

FIG. 2. Projection des 15 axes-groupes des trois stations de juin 1979, dans le plan réduit des deux premiers axes principaux. Les taxons dont la longueur de la projection égale ou excède le rayon du cercle de contribution équilibrée ($\sqrt{2/15}$ = 0,365) contribuent à la formation de l'espace réduit étudié. 1: *Mallotus villosus*; 2: *Osmerus mordax*; 3: *Clupea harengus harengus*; 4: Pisces (larves); 5: *Meganictiphanes norvegica*; 6: *Thysanoessa* sp.; 7: Mysidacés (adultes); 8: Mysidacés (juvéniles); 9: Copépodes (> 2 mm); 10: Microplancton (≤ 2 mm); 11: *Sagitta elegans*; 12: Amphipodes; 13: Polychètes errants; 14: Décapodes (larves); 15: Pisces (œufs). Les axes principaux sont identifiés par les descripteurs du milieu avec lesquels ils sont fortement corrélés.

cipaux parvient cependant à expliquer 60,3% de la variance totale observée (Tableau 3). Parmi les 15 groupes représentés, seul le microplancton participe peu à la formation de l'espace réduit étudié (corrélation < 0,365; Fig. 2) et sera ignoré dans l'étape suivante de l'analyse.

Les groupes qui contribuent de façon prépondérante à la formation du premier axe principal (Tableau 3) sont les larves de poisson non identifiées (Pisces), les euphausiacés (deux genres), les mysidacés juvéniles, les copépodes >2 mm et *Sagitta elegans* de même que, à un degré moindre, les larves de capelan, les mysidacés adultes, les amphipodes, les polychètes errants et les larves de décapodes. Les groupes contribuant davantage à la formation de l'axe principal II sont les larves d'éperlan et de hareng, les larves de décapodes et les œufs de poisson.

L'ordination des échantillons dans le plan réduit des deux premiers axes principaux (Fig. 3) permet de juger de la position relative des stations par rapport aux axes d'ordination. Le calcul et le positionnement des centroides des strates de chaque station permet de visualiser l'emplacement des échantillons de chaque couche. Ces observations permettent donc de situer l'axe de l'estuaire de même que l'axe vertical (surface-fond) sur cette figure. L'axe principal I permet d'isoler la station aval (79-3) bien qu'il existe un certain degré de chevauchement entre les échantillons de cette station et les échantillons de surface (0−20 m) de la station médiane (79-2). L'axe principal II assure la séparation de la station amont 79-1. De plus, l'étude de la position des centroides des échantillons de chaque strate, permet de constater que la composition planctonique est très homogène sur toute la colonne d'eau à la station 79-3, en raison de la proximité des centroïdes. Par contre, à la station 79-2, la couche de surface (0−20 m) se détache des deux strates profondes (20−40 m; 40−60 m) indiquant une forte hétérogénéité biologique entre la première d'une part et les deux autres, plutôt homogène,

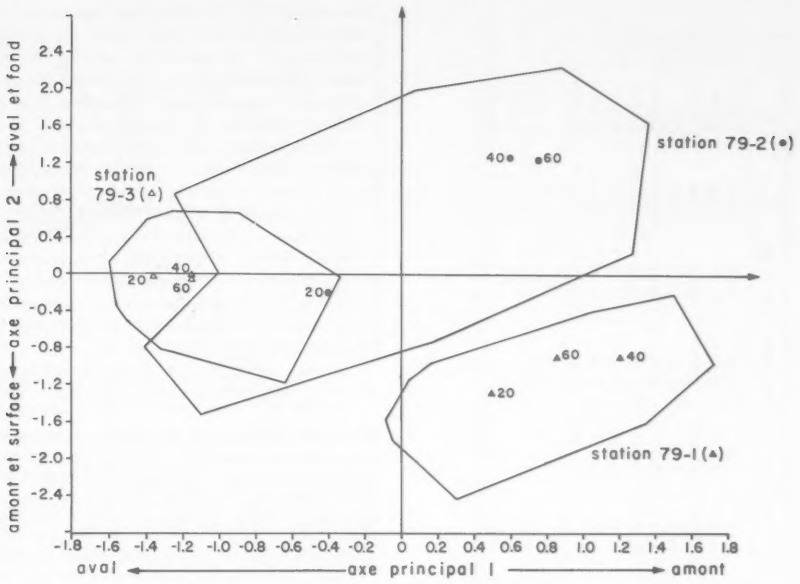

FIG. 3. Ordination des échantillons des trois stations de juin 1979 dans le plan réduit formé par les deux premiers axes principaux. Les traits pleins délimitent la dispersion des échantillons de chaque station. Les échantillons prélevés à l'intérieur d'une même couche sont représentés par leur centroïde (moyenne arithmétique des échantillons de cette couche). Le symbole utilisé pour indiquer les centroïdes d'une même station apparaît entre parenthèses après le numéro de la station. Les axes principaux sont identifiés par les descripteurs du milieu avec lesquels ils sont fortement corrélés.

d'autre part. La station amont 79-1 montre sensiblement le même phénomène mais de façon moins marquée.

L'interprétation des axes d'ordination par les variables physiques du milieu (Tableau 4) indique que la latitude, la longitude, l'indice de turbidité (Secchi), la température de surface, l'indice de stratification ($\Delta\sigma_{t5-35}$) et la profondeur échantillonnée sont significativement corrélés à la composante principale I. Le calcul de corrélations partielles, permettant d'éliminer l'effet de la latitude (ou de la longitude), diminue de façon marquée la corrélation entre l'indice de Secchi ($\tau = -0{,}18$), la température de surface ($\tau = 0{,}11$) et l'indice de stratification ($\tau = 0{,}27$) avec la première composante principale. La relation entre ces trois variables du milieu et la répartition spatiale des groupes planctoniques n'est, par conséquent, pas indépendante de leur répartition en fonction de la position géographique des stations d'échantillonnage. À ce titre, il est permis de croire que l'axe I (Fig. 3) ordonne les échantillons selon un gradient caractéristique de certaines masses d'eau. Sur la partie gauche de l'axe principal I se trouvent les masses d'eau d'aval froides, claires et peu stratifiées (station 79-3 et 79-2 (0–20 m)), auxquelles sont associées les larves de poisson non identifiées, les larves de capelan, les larves de décapodes et celles de hareng (corrélations négatives avec l'axe I, Tableau 3 et Fig. 2). Par contre, sur la partie droite de l'axe principal I (Fig. 3) se retrouvent les masses d'eau de l'amont de l'estuaire plus chaudes, plus turbides et plus stratifiées (station 79-1 et 79-2 (20–60 m)), auxquelles sont associées le macroplancton (copépodes >2 mm, euphausiacés, mysidacés, chaetognathes, et amphipodes) de même que les polychètes errants et les larves d'éperlan (corrélations positives avec l'axe I, Tableau 3 et Fig. 2).

Les paramètres physiques significativement corrélés à la composante principale II sont la température, la salinité, la densité (σ_t), la latitude, la longitude, l'indice de turbidité, la température de surface, l'indice de stratification et la profondeur échantillonnée (Tableau 3). L'utilisation de corrélations partielles, permettant de contrôler l'effet de la profondeur, abaisse de façon sensible les corrélations de la température ($\tau = -0{,}13$), de la salinité ($\tau = 0{,}08$) et de la densité ($\tau = 0{,}08$) avec la deuxième composante principale. Une tendance similaire est observée lorsque l'effet de la position des stations est contrôlé lors du calcul des corrélations entre ces mêmes variables et la composante II ($\tau = -0{,}17, +0{,}10; +0{,}10$ respectivement). Ainsi, il semble que la relation entre la température, la salinité, la densité et la distribution spatiale des groupes planctoniques ne soit pas indépendante de leur distribution selon la profondeur. Par contre, cet axe d'ordination ne peut être dégagé de toute influence spatiale vu les corrélations significatives enregistrées avec la position géographique, la température de surface, l'indice de Secchi et l'indice de stratification. L'axe II semble donc représenter un ensemble de facteurs qui varie avec la profondeur de la station 79-1 à la station 79-2 qui sont les deux stations que cet axe

TABLEAU 4. Matrice des corrélations (τ de Kendall) entre les variables échantillonnées aux stations 79-1, 79-2 et 79-3 en juin 1979. C_1 et C_2 sont les deux premières composantes principales. Le chiffre entre parenthèses indique le nombre d'observations (n). (* $0{,}01 < P \leq 0{,}05$; ** $P \leq 0{,}01$.)

	Salinité	Densité	Heure	Latitude	Longitude	Éclairement	Secchi	T° surface	$\Delta\sigma_{t5-35}$	Profondeur	Amplitude	C_1	C_2
Température (95)	−0,89**	−0,90**	0,09	−0,31**	0,31**	−0,05	−0,21*	0,15*	0,12	−0,69**	0,03	0,01	−0,25**
Salinité (95)		0,99**	−0,10	0,41**	−0,41**	0,06	0,30**	−0,22**	−0,18**	0,65**	−0,05	−0,08	0,21**
Densité (95)			−0,10	0,40**	0,40**	0,06	0,30**	−0,22**	−0,18**	0,65**	−0,05	−0,08	0,21**
Heure (121)				−0,02	0,03	0,35**	−0,09	0,13*	0,04	−0,09	−0,27**	0,02	−0,06
Latitude (121)					−0,99**	0,05	0,88**	−0,73**	−0,53**	0,09	0,01	−0,63**	0,31**
Longitude (121)						−0,06	−0,88**	0,73**	0,53**	−0,09	−0,01	0,63**	−0,32**
Éclairement (121)							−0,10	0,00	−0,11	0,00	−0,17**	−0,11	0,00
Secchi (63)								−0,70**	−0,53**	0,05	0,34**	−0,62**	0,29**
T° surface (101)									0,64**	−0,06	−0,23**	0,52**	−0,24**
Stratification ($\Delta\sigma_{t5-35}$) (95)										−0,02	0,07	0,51**	0,25**
Profondeur (120)											0,04	0,14*	0,23**
Amplitude (121)												−0,01	0,10*

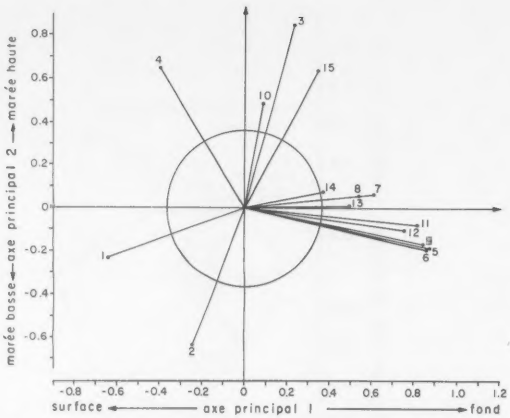

FIG. 4. Projection des 15 axes-groupes de la station médiane 79-2 dans le plan de plus grande variance (deux premiers axes principaux). Tous les taxons contribuent à la formation de l'espace réduit étudié (projections supérieures au rayon du cercle de contribution équilibrée : $\sqrt{2/15} = 0{,}365$). Les chiffres représentent les mêmes groupes qu'à la figure 2. Les axes principaux sont identifiés par les descripteurs du milieu avec lesquels ils sont fortement corrélés.

parvient à séparer (Fig. 3). La figure 2 montre que les larves d'éperlan, les polychètes errants et les mysidacés (juvéniles) sont plus représentatifs des masses d'eau qui caractérisent la station 79-1 (Fig. 3), alors que le reste du macroplancton est plus représentatif des masses d'eau qui caractérisent la couche profonde (20−60 m) de la station 79-2 (Fig. 3).

ORGANISATION SPATIALE À LA STATION MÉDIANE

Afin de complémenter les résultats obtenus, une analyse en composantes principales a également été menée sur les données biologiques recueillies à la station montrant la plus grande variabilité dans la composition et l'abondance relative des organismes (79-2; Fig. 3). Cette analyse a permis de mettre en évidence l'organisation de la communauté de même que les principaux facteurs responsables de la variabilité à petite échelle.

Le modèle de Frontier (1976) révèle, ici également, que seules les deux premières composantes principales extraites de la matrice de corrélations sont interprétables. Le plan formé par les deux premiers axes principaux suffit cependant à expliquer 51,1% de la variance totale (Tableau 3).

La figure 4 représente la projection des 15 axes-groupes dans le plan des deux premiers axes principaux. Les groupes qui contribuent davantage à la formation de l'axe principal I (Tableau 3) sont les euphausiacés (*M. norvegica* et *Thysanoessa* sp.), les copépodes >2 mm, les chaetognathes, les amphipodes, les mysidacés et les larves de capelan. Les polychètes errants, les larves de décapodes et les larves de poisson non-identifiées contribuent également à la formation de cet axe mais plus faiblement. Les groupes principalement associés à l'axe principal II sont les larves de hareng, les larves de poisson nonidentifiées, les œufs de poissons, les larves d'éperlan et, plus faiblement, le microplancton.

La première composante principale est significativement corrélée (Tableau 5) à la composante u du courant de marée, à la température, la salinité, la densité (σ_t), la profondeur et l'indice de stratification ($\Delta\sigma_{t5-35}$). Ici aussi des corrélations partielles sont nécessaires pour dégager la structure fondamentale vu le grand nombre de variables corrélées (Tableau 5). Ainsi, le lien entre la composante principale I et le complexe température−salinité−densité dépend surtout de la profondeur, puisque l'exclusion de cette variable du calcul de la corrélation entre la température ou la salinité et la première composante a un effet plus marqué ($\tau = -0{,}17$) que le retrait de la composante u du courant ($\tau = -0{,}42$). De plus, la corrélation significative observée entre la composante u du courant et la composante principale I disparaît si l'on exclut l'effet de la température ou de la salinité du calcul de la corrélation ($\tau = -0{,}10$). Par conséquent, la relation entre la distribution spatiale des groupes et le complexe température−salinité−densité semble dépendante de leur répartition en fonction de la profondeur.

La composante principale II est significativement corrélée à l'indice de turbidité (Secchi), à la température de surface, à l'éclairement, au complexe température−salinité−densité, à l'indice de stratification et à l'amplitude de la marée. La distribution des groupes dans le milieu paraît donc influencée par le phénomène de la marée (oscillation des masses d'eau) auquel sont liés le complexe température−salinité−densité, ainsi que la turbidité et la température de surface.

La figure 5 représente l'ordination des échantillons dans le plan réduit des deux premiers axes principaux à laquelle est superposé le groupement à liens complets. L'axe principal I permet de séparer la plupart des échantillons de la couche de surface (0−20 m; échantillons 1 à 16), de ceux provenant des couches plus profondes (20−40 m, 17 à 32; 40−60 m, 33 à 48). Le groupement à liens complets, quant à lui, délimite trois groupes. Les deux plus grands sont reliés à l'axe principal I (profondeur), alors que le troisième est associé à l'axe principal II et semble ainsi lié aux fortes amplitudes de marée.

L'analyse en composantes principales met donc en évidence l'importance de la structure physique verticale de la colonne d'eau (composante I = 34,9% de la variance). Son influence est surtout marquée pour le macroplancton qui occupent les couches profondes, de même que pour les larves de capelan et les larves de poisson non identifiées qui se retrouvent majoritairement dans la couche superficielle (Fig. 4). Par contre les phénomènes liés aux courants de marés sont les principaux facteurs de variation pour les larves de poisson (sauf le capelan) de même que pour les œufs de poisson et le microplancton. Ces groupes se trouvent davantage associés aux masses d'eau de l'aval, à l'exception des larves d'éperlan qui habitent les eaux plus douces, plus chaudes et plus turbides de l'amont.

Les deux premières composantes principales illustrent les tendances les plus importantes de la variabilité observée. Les résultats obtenus ne signifient pas cependant que les espèces associées à l'axe principale I ne sont pas influencées par les phénomènes de marée, mais que cette influence est beaucoup moins importante. À titre d'exemple, l'axe principal I explique environ 49,7% (±23,8) de la variance observée chez le macroplancton tandis que l'axe principal II n'en explique seulement 1,4% (±1,4).

TABLEAU 5. Matrice des corrélations (τ de Kendall) entre les variables physiques recensées à la station 79-2 en juin. C_1 et C_2 représentent les deux premières composantes principales. Le chiffre entre parenthèses indique le nombre d'observations (n). (*$0{,}01 < P \leq 0{,}05$; ** $P \leq 0{,}01$.)

	Secchi	T° surface	Eclairement	u	v	Température	Salinité	σ_t	Profondeur	$\Delta\sigma_{t5-35}$	Amplitude	C_1	C_2
Heure (48)	−0,19	0,35**	0,10	0,33**	−0,07	0,07	−0,08	−0,08	−0,03	0,09	−0,31**	0,02	−0,10
Secchi (27)		0,00	−0,44**	0,49**	−0,13	−0,02	0,03	0,03	−0,05	0,00	−0,29*	−0,23	0,40**
T° surface (39)			−0,28	0,02	0,09	0,01	−0,01	−0,01	0,05	0,51**	−0,14	0,15	−0,26*
Eclairement (48)				−0,01	−0,02	−0,01	0,02	0,02	−0,04	−0,12	0,12	−0,02	0,19*
Composante u du courant (48)					−0,09	0,25**	−0,24**	−0,24**	−0,12	−0,21*	−0,57**	−0,20*	−0,05
Composante v du courant (48)						−0,13	0,12	0,12	0,02	0,22*	0,20*	0,00	0,09
Température (48)							−0,96**	−0,96**	−0,64**	−0,07	−0,17*	−0,45**	−0,23*
Salinité (48)								0,99**	0,62**	0,08	0,17*	0,46**	0,24*
Densité (σ_t) (48)									0,62**	0,08	0,16*	0,45**	0,24*
Profondeur (48)										0,07	0,25**	0,53**	0,14
Stratification ($\Delta\sigma_{t5-35}$) (48)											−0,05	0,17*	−0,18*
Amplitude de la marée (48)												0,06	0,16*

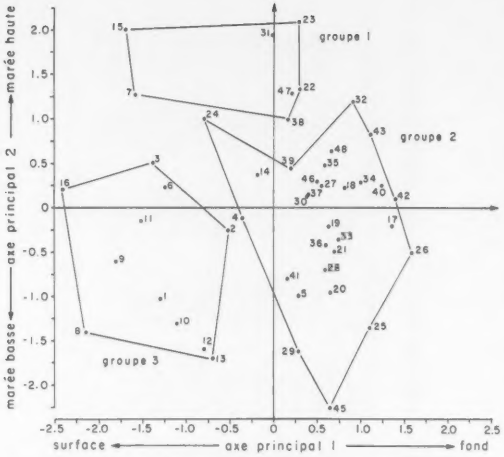

FIG. 5. Ordination des échantillons de la station médiane 79-2 dans le plan de plus grande variance. Les traits continus délimitent les groupes formés par groupement à liens complets (distance euclidienne < 3,77). N° 1 à 16: échantillons 0−20 m; n° 17 à 32: échantillons 20−40 m; n° 33 à 48: échantillons 40−60 m. Les axes principaux sont identifiés par les descripteurs du milieu avec lesquels ils sont fortement corrélés.

Bien que l'éclairement, également associé à l'axe principal II, n'explique pas un grand pourcentage de la variance du macroplancton, il n'en demeure pas moins un facteur lié aux mouvements effectués par le zooplancton. Les fluctuations d'abondance des euphausiacés, des chaetognathes et des amphipodes aux différentes couches échantillonnées (Tableau 6) ne sont pas indépendantes de l'éclairement (chi-carré, $P < 0{,}001$ pour chaque tableau de contingence). Par conséquent, la plus grande abondance en surface la nuit du macroplancton semble donc résulter des migrations nycthémérales de ces organismes.

Discussion

ORGANISATION SPATIALE À L'ÉCHELLE DE L'ESTUAIRE MOYEN

La présente étude met en relief la distribution non aléatoire des organismes dans la partie étudiée de l'estuaire moyen du Saint-Laurent. Les groupes recencés se distribuent de façon contagieuse autant selon l'axe horizontal que vertical et cette distribution est également influencée par les effets de marée. Ainsi, la station médiane contient les plus fortes densités de macroplancton, particulièrement concentrées dans la couche profonde (20−60 m). La station amont est surtout caractérisé par l'abondance des larves d'éperlan, des mysidacés juvéniles et des polychètes errants, tandis que les larves de poisson (à l'exception de l'éperlan) et les larves de décapodes se trouvent davantage à la station aval (Tableau 1 et Fig. 2).

L'estuaire moyen du Saint-Laurent est partiellement mélangé, constituant un système de circulation en deux couches maintenu par l'avancement en profondeur d'eau marine vers l'amont (Bousfield et al. 1975; Gagnon et Lacroix 1981). Cette séparation de la colonne d'eau se reflète également dans la distribution des organismes planctoniques. Les échantillons de la couche de surface (0−20 m) se détachent sensiblement de ceux de la couche profonde (20−60 m) par leur composition biologique, tout au moins aux deux stations amont 79-1 et 79-2 (Fig. 3). Au niveau de la station aval toutefois, l'estuaire moyen devient moins stratifié (D'Anglejan et Smith 1973). Ce changement physique est probablement responsable de l'homogénéité biologique de la colonne d'eau observée à la station 79-3, puisque l'absence d'une forte stratification contribue à accentuer l'homogénéisation de la colonne d'eau.

Les trois stations échantillonnées diffèrent passablement quant à leur composition planctonique (Tableau 1 et Fig. 3), mais la couche de surface de la station médiane (79-2) montre une certaine ressemblance avec les échantillons de la station aval (79-3). De fait, tous ces échantillons sont caractérisés par des densités élevées de larves de capelan et par de faibles densités de macroplancton. Ce lien biologique qui unit la couche supérieure de la station 79-2 à la station 79-3 souligne bien l'hétérogénéité de la station médiane.

ORGANISATION SPATIO-TEMPORELLE À LA STATION MÉDIANE

La différence qui existe entre la composition biologique de la plupart des échantillons de surface (0−20 m) et celle des échantillons de la couche profonde (20 − 60 m) est révélée de façon plus nette encore par l'analyse réalisée à l'échelle de cette station. Les groupes 2 et 3 (Fig. 5), obtenus suite à la superposition du groupement à l'ordination des échantillons, illustrent bien ce point. De plus, l'analyse met en évidence un autre groupe (groupe 1) associé aux fortes amplitudes de marée. Ce groupe paraît hétérogène a priori puisqu'il comprend des échantillons provenant des trois couches échantillonnées. Par contre, ces derniers ont tous été recueillis aux environs des amplitudes quotidiennes maximales de la marée. Le groupe 1 représente donc un ensemble d'échantillons prélevés dans une masse d'eau de l'aval, amenée à la station 79-2 à toutes les 24 h par les plus fortes amplitudes de la marée. Pour cette section de l'estuaire, Gagnon et Lacroix (1981) estiment que les déplacements des masses d'eau sont de l'ordre d'une vingtaine de kilomètres en période de vive-eau. Cette advection est donc suffisante pour amener périodiquement à la station médiane des masses d'eau de l'aval.

Dans la portion aval de l'estuaire moyen, la variabilité à l'intérieur d'une station est parfois aussi importante que la variabilité entre les stations en ce qui a trait à la composition planctonique. Cette forte variabilité observée selon la profondeur semble causée par le mode de circulation en deux couches des eaux de l'estuaire. Ce système a des répercussions marquées sur la distribution de certains organismes qui se trouvent majoritairement dans l'une des couches, comme l'a mis en évidence l'analyse en composantes principales menée sur les échantillons de la station 79-2 (Fig. 4). À cette station, la profondeur est la principale source de variation d'abondance pour les larves de capelan (surface) et le macroplancton (profondeur); toutes les autres larves de poisson, les larves de décapodes et le microplancton montrent des fluctuations plus importantes selon la marée. Conte et al. (1979) ont eux aussi rapporté d'importantes fluctuations d'abon-

TABLEAU 6. Abondance relative des euphausiacés (*M. norvegica* et *Thysanoessa* sp.), du chaetognathe (*S. elegans*) et des amphipodes en fonction de l'éclairement et de la profondeur à la station 79-2. Les probabilités inconditionnelles représentent l'abondance relative de chacun des groupes pour l'ensemble de la colonne d'eau dans les différentes conditions d'éclairement. J, jour; P, pénombre; N, nuit. Les probabilités conditionnelles (abondance relative par couche et condition d'éclairement) qui dépassent la probabilité inconditionnelle sont soulignées.

	M. norvegica			*Thysanoessa* sp.			*S. elegans*			Amphipodes		
	J	P	N	J	P	N	J	P	N	J	P	N
Probabilité inconditionnelle	0,68	0,16	0,16	0,54	0,24	0,22	0,59	0,20	0,21	0,72	0,04	0,24
0−20 m	0,04	0,13	0,83	0,25	0,13	0,62	0,57	0,09	0,35	0,00	0,20	0,80
20−40 m	0,59	0,25	0,16	0,52	0,38	0,10	0,61	0,22	0,17	0,83	0,03	0,14
40−60 m	0,82	0,10	0,08	0,65	0,08	0,26	0,56	0,18	0,25	0,67	0,04	0,28

dance selon l'état de la marée pour l'ichtyoplancton de la baie Chesapeake où les amplitudes de la marée sont quelque 10 fois moins prononcées (≈0.5 m) que dans l'estuaire moyen du Saint-Laurent.

INTERACTIONS MULTISPÉCIFIQUES

Les données concernant la distribution du macroplancton dans le secteur étudié laissent entrevoir la possibilité de compétition et de prédation des jeunes larves de poisson par les chaetognathes, les euphausiacés et les amphipodes, principalement aux stations amont et médiane (Tableaux 1 et 2). Même si les larves de capelan sont séparées du macroplancton sur le plan vertical, il n'en demeure pas moins que ce dernier pourrait, lors de ces migrations nocturnes vers la surface (Tableau 6), exercer une pression de prédation sur les larves de capelan, très petites en juin (environ 4−5 mm). Les larves de hareng peuvent également subir une certaine prédation à la station médiane à cause de leur plus grande abondance en profondeur et de leur petite taille en juin (<10 mm). Sinderman (1979) mentionne à ce propos que les larves de hareng plus petites que 15 mm ont une faible capacité natatoire puisque leur nageoire caudale n'est pas encore formée. Les larves d'éperlan risquent moins d'être touchées par cette prédation en raison de leur grande taille (environ 13 mm) et de leur plus grande abondance dans les eaux moins salées.

L'étude de l'organisation spatio-temporelle de la communauté planctonique, réalisée à deux échelles, démontre que les larves de poisson sont distribuées dans le milieu de telle sorte que sont minimisées les interactions. Tel qu'indiqué, les larves d'éperlan qui sont plus caractéristiques des masses d'eau de l'amont (79-1), sont séparées des larves de capelan et de hareng plus typiques des masses d'eau de l'aval (79-3) à cette période de l'année. De plus, l'étude de la structure de la communauté à plus petite échelle (79-2) révèle que les larves de capelan sont plus abondantes en surface (0−20 m) alors que les larves de hareng sont plus nombreuses dans la couche profonde (20−60 m). Donc, l'impact des relations multispécifiques sur la croissance et le recruitement des poissons tel que suggéré par Lett et Kohler (1976) et Winters (1976) ne peut pas être démontré au niveau larvaire. Nos résultats indiquent que dans un milieu estuarien, la salinité et la température, de concert avec d'autres facteurs du milieu, présentent un gradient horizontal et vertical marqué qui module la distribution et l'abondance des organismes, assurant ainsi leur séparation écologique.

Larkin (1956) et Sale (1977) décrivent le partage de l'habitat (« habitat partitioning ») comme étant un moyen de réduire la compétition chez les populations de poissons d'eau douce. Il semble qu'un mécanisme semblable puisse agir dans le cas de l'ichtyoplancton de l'estuaire moyen du Saint-Laurent. La séparation observée, maintenue par les facteurs physiques du milieu, semble la conséquence de stratégies différentes de reproduction. En effet, Jacquaz et al. (1977) rapportent que les larves de capelan sont transportées en aval par les courants de surface, de leur site de frai sur les berges de l'estuaire moyen à une aire d'alimentation située dans la région nord-ouest du golfe du Saint-Laurent. À l'opposé, les larves de hareng semblent utiliser les courants résiduels vers l'amont en profondeur pour passer de leur aire d'éclosion située entre l'île aux Lièvres et l'île Verte à leur site d'alimentation localisé plus haut en amont entre l'île aux Coudres et l'île aux Lièvres (Able 1978).

Finalement, les larves d'éperlan sont remises en circulation à partir de certains tributaires du Saint-Laurent situées à la hauteur et en amont de l'île aux Coudres. Elles peuvent se maintenir dans cette région de l'estuaire en raison de leur distribution côtière après l'éclosion (Marcotte et Tremblay 1948) et, plus tard, par l'utilisation de la circulation résiduelle vers l'amont (Able 1978).

Les résultats obtenus démontrent que les probabilités d'interactions entre les larves de capelan, d'éperlan et de hareng sont plutôt faibles dans l'estuaire moyen du Saint-Laurent. Toutefois, une étude du régime alimentaire et de la croissance de ces larves est requise avant de conclure qu'il n'existe entre ces espèces aucune interaction pouvant affecter leur croissance, leur mortalité et par conséquent, leur recrutement au sein des populations adultes.

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Structuring of a Predator Population Through Temperature-Mediated Effects on Prey Availability[1]

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ADAMS, S. M., R. B. MCLEAN, AND M. M. HUFFMAN. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Can. J. Fish. Aquat. Sci. 39: 1175 – 1184.

Temperature can control the structure of a predator population by regulating the abundance and size availability of prey. Relatively small differences in winter temperatures between years can have a major influence on largemouth bass (*Micropterus salmoides*) population structure because of the threshold relationship between temperature and the lower lethal limits of shad. The relationship between prey availability and predator growth and mortality was established through field measurements of consumed energy. Growth and consumption of largemouth bass in Watts Bar Reservoir, Tennessee, was lower in 1979 than in 1980 as a result of lower winter water temperature in 1979, which reduced the abundance and availability of adequate-sized prey. Depending on the severity of the winter, bass that do not attain 25 ± 5 cm by the end of their first growing season do not survive to annulus I formation because of the unavailability of appropriate-sized prey in the spring and the inability of small bass to store sufficient energy reserves. Selective mortality favoring survival of larger individuals in an age-class is operating in the Watts Bar largemouth bass population. This has significant implications for predator growth in ecosystems that experience large seasonal fluctuations in prey availability.

Key words: predator population structure, prey availability, reservoir temperature, energy consumption, growth, largemouth bass, selective mortality, shad

ADAMS, S. M., R. B. MCLEAN, AND M. M. HUFFMAN. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Can. J. Fish. Aquat. Sci. 39: 1175 – 1184.

La température peut contrôler la structure d'une population de prédateurs par régulation de l'abondance et de la disponibilité de taille des proies. Des différences relativement faibles des températures hivernales d'une année à l'autre peuvent influer beaucoup sur la structure des populations d'achigans à grande bouche (*Micropterus salmoides*) par suite de la relation de seuil qui existe entre la température et les limites létales inférieures de l'alose savoureuse. Des mesures sur le terrain de l'énergie consommée ont permis d'établir la relation entre la disponibilité des proies et la croissance et la mortalité des prédateurs. La croissance et la consommation d'achigans à grande bouche dans le réservoir de Watts Bar, dans le Tennessee, étaient plus faibles en 1979 qu'en 1980 par suite d'une température de l'eau en hiver plus basse en 1979, qui causa une diminution de l'abondance et de la disponibilité de proies de taille convenable. Selon la sévérité de l'hiver, les achigans qui n'ont pas atteint 25 ± 5 cm à la fin de leur première saison de croissance mourront avant formation de l'annulus I parce qu'il n'y a pas de proies de taille convenable au printemps et que les petits achigans ne peuvent stocker des réserves énergétiqus suffisantes. Il y a dans la population d'achigans à grande bouche de Watts Bar une mortalité sélective qui favorise la survie des grands sujets d'une classe d'âge. Ceci a d'importantes implications sur la croissance des prédateurs dans des écosystèmes où la disponibilité des proies accusent de fortes fluctuations saisonnières.

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TEMPERATURE can influence the dynamics of fish populations through control of physiological processes (Fry 1971), control of behavioral thermoregulation (Coutant 1977), interaction with toxicants (Cairns et al. 1975), effects on spawning and survival of early life stages (Summerfelt 1975), and promotion of disease (Reichenbach 1974). Temperature also may exert a regulating influence on the structure of predator populations by controlling the density, size availability, and quality of prey available to a predator. In many large freshwater systems of North America, threadfin shad (*Dorosoma petenense*) and gizzard shad (*Dorosoma cepedianum*), the primary forage of several predators experience cold-stress mortality when water temperatures drop below 9°C, with complete mortality occurring around 4°C (Griffith 1978; McLean et al. 1980). When mass winter mortalities (Hassler 1953; Parsons and Kimsey 1954; McLean et al. 1980) or even partial mortality of forage populations occur, predators are usually faced with a shortage of their preferred food during the spring and early summer. Response of predator populations to severe seasonal or yearly fluctuations in prey abundance is not well documented. In northern systems, reduction in growth rate and fecundity of sauger (*Stizostedion canadense*) and walleye (*Stizostedion vitreum vitreum*) has been attributed to winter kill of gizzard shad (Forney 1965; Nelson 1969). Minton et al. (1981) stated that sauger in a southeastern reservoir cope with large seasonal variations in threadfin shad availability by increasing their consumption (over prewinter levels) of vulnerable cold-stressed shad in early winter and storing this excess energy in large fat deposits which are metabolized in the spring and early summer when shad are scarce.

The objective of this study was to determine if temperature influences the size structure of a predator population by affecting the size of the predator's preferred prey. We measured growth, mortality, and food consumption of largemouth bass (*Micropterus salmoides*) as possible variables which are affected by both a fluctuating prey base and size availability of prey. We chose largemouth bass for this study because of its importance as a game fish throughout North America and our hypothesis that a fluctuating prey base is an indirect determinant of bass growth and survival. This is the first study on adult largemouth bass where the effects of temperature on population structure, mediated through prey availability, have been investigated and where energy consumption has been measured for natural populations.

Methods

This study was conducted in Watts Bar Reservoir, a 13 300-ha impoundment of the Tennessee River in eastern Tennessee. The reservoir, characterized by shallow flats about the main channel which stratifies during the summer, is a mesotrophic system with a diversity of native and introduced fish species. Threadfin and gizzard shad are the dominant forage species in the reservoir, while largemouth and smallmouth bass (*Micropterus dolomieui*), sauger, striped bass (*Morone saxatilis*), and white bass (*Morone chrysops*) are the principal predators. The shad populations, and particularly the threadfin, undergo dramatic temporal fluctuations in abundance, due primarily to winter cold-kill (McLean et al. 1980).

We collected largemouth bass biweekly in 1979 and 1980 by electroshocking with equal effort in brush piles, submerged vegetation, and rocky shores. Electrofishing is a relatively nonselective method of sampling all size-classes of largemouth bass in a population (Woodrum 1974; Frankenberger 1960). A minimum of 35 bass (ages I^+ and older) were captured each month, except when unfavorable water temperatures (<10°C and >27°C) forced bass into deep water. Fish were frozen immediately with dry ice to stop digestion. Prey species also were collected, by electroshocking, for caloric and ash analysis.

Total lengths, weight, and viscera weights were recorded, scales removed, and stomach contents analyzed for all bass. Two bass from each age-group were saved each month for caloric and ash analysis of whole body and viscera. Lengths (total, standard, or backbone) and weights of ingested prey were recorded and partially digested prey were identified by the presence of gizzards, otoliths, or dorsal spines.

We determined the caloric content of whole bass (carcass, viscera, and gonads), viscera, and representative prey each month with a Parr adiabatic bomb calorimeter following standard methods (Paine 1971). Samples were freeze-dried, ground into a homogeneous mixture with a Wiley mill, and two subsamples combusted from each sample. To determine sample replicability, seven replicates each of samples with high ash (27%) and low ash (8%) were analyzed yielding caloric values of 4.028 ± 0.063 and 6.487 ± 0.061 cal·g^{-1}, respectively. Because of this precision, we subsequently ran only two determinations per sample. Ash contents were determined from duplicate subsamples of fish tissue ignited for 18 h at 500°C.

For digestion rate studies, field-collected 400 to 700-g bass were individually placed in 1-m^3 vexar mesh cages in large circular tanks supplied with running well water with computer-controlled temperatures. Bass were held in the laboratory for 6 wk before the digestion experiments, and were fed large fathead minnows (*Pimephales promelas*). Digestion rate experiments were run at 14, 17, 20, 23, 26, and 28°C, spanning the range of temperatures at which bass were observed to feed in the field. We did not feed bass 36 h prior to experiments, and experiments were conducted 2 wk apart to allow normal feeding to resume. For each experiment, 25–30 fish were each fed 2% of their body weight (mean field daily ration determined by consumption measurements). Only bass that fed voluntarily were used in the experiments, because force-feeding has been shown to bias digestion rates (Swenson and Smith 1973). At various intervals following feeding, and depending on temperature, three to four bass were anesthetized with MS-222 and their stomachs gently pumped (Seaburg 1957). We calculated time to 95% digestion at each temperature by a regression of the fraction digested at each sample interval against hours following feeding. Time to 95% digestion was considered the endpoint of digestion because the remaining 5–10% is considered the residual phase where digestion of hard parts is slowed significantly (Swenson and Smith 1973). Digestion rate of live threadfin shad was also conducted at two temperatures and the time to 95% digestion compared to minnows using Student's *t*-test and the Satterthwaite (1946) procedure to approximate the degrees of freedom.

We calculated monthly consumption or daily ration of bass in the field by the relationship

$$C = \frac{\sum_{i=1}^{n} (Pw_i / Bw_i}{n},$$

where: C = consumption or daily ration ($mg \cdot g^{-1} \cdot d^{-1}$), Pw_i = weight of prey ingested during a defined 24-h period, Bw_i = weight of bass that consumed prey Pw_i, and n = number of bass in sample including those with empty stomachs. Monthly ration estimates ($mg \cdot g^{-1} \cdot d^{-1}$) were calculated for each age-class ($I^+ - IV^+$), converted to consumed energy ($cal \cdot g^{-1} \cdot d^{-1}$) by accounting for prey caloric value, and these monthly values summed to yield annual rations for each age-class.

Prey ingested during 24 h was determined from the digestion rate of prey given the temperature and time of bass capture, original weight of an ingested prey, and time of prey ingestion. Temperature was taken in each general area in which bass were captured. Digestion rate of prey at any reservoir temperature was determined from a regression of time to 95% digestion at the six temperatures tested in the laboratory. We calculated original weights of ingested prey from a series of backbone length, standard length, and total length regressions (Minton et al. 1981). Time of ingestion was determined by backcalculating, from the time of capture, the number of hours that the prey had been in the stomach based on stage of digestion. Stage of digestion (proportion digested) was calculated as 1 − (digested weight/original weight). A bass was given credit for consuming prey only if the prey was ingested within a designated period which included 24 h previous to the capture of the last bass. When digestion rate was greater than 24 h, food in the stomach was a record of ingestion 24 h prior to capture. If digestion rate was less than 24 h, we sampled twice (12 h apart) within a 24-h period and combined fish from both sampling periods to account for those bass that fed within the 24 h but may have digested their meal before capture.

We determined age of bass by analyzing scales taken from the body near the tip of the left pectoral fin. Lengths at each annulus were backcalculated by substituting the intercept values of the total length−anterior radius relationship into the expression

$$BL = I + (S'/S)\,(TL - I),$$

where: BL = backcalculated length at annulus, I = intercept of the length−scale radius equation, S' = annulus distance, S = scale radius, and TL = total length of fish. The intercept (I) was calculated by a geometric means regression procedure of Ricker (1973) which minimized both the vertical and horizontal regression sum of squares. Weight-specific caloric growth ($cal \cdot g^{-1} \cdot d^{-1}$) for a month was calculated as the mean weight-specific caloric content of the whole fish ($cal \cdot g^{-1}$) during that month times the mean weight gain over the month divided by the monthly mean weight.

Prey size−frequency distribution over the year was determined from biweekly gillnetting data of Minton et al. (1981) collected from April 1979 to March 1980. Weekly impingement data were collected by McLean et al. (1980) from the intake screens of Kingston Steam Plant on Watts Bar Reservoir during the winters of 1976−80. Biweekly surface and mid-depth (3 m) temperatures were taken at several areas of the reservoir, including cove and main reservoir stations.

Results

Temperature

The winter of 1979 was colder than the winter of 1980. During January and February of 1979, temperatures averaged 4−5°C with one week in February reaching 2.9°C. During the winter of 1980, temperatures ranged between 7 and 10°C, except for one week that averaged 6.4°C. Summer water temperatures were also higher in 1980, with highs reaching 30°C for two weeks in August 1980 and 27.5°C in August 1979.

Growth and Size Changes

Caloric growth and growth in size of bass were generally greater in 1980 than in 1979 (Table 1). Caloric gain of an average age I^+ and II^+ bass was 3.5 and 1.7 times greater, respectively, in 1980 than in 1979 while caloric growth of age III^+ was about the same both years. The average weights at the end of the growing season were 1.8, 1.4, and 1.2 times greater for ages I^+, II^+, and III^+, respectively, in 1980 compared to 1979.

Backcalculation to determine size at each annulus formation for various year-classes of bass revealed that backcalculated lengths were larger than observed lengths for each respective age. There is a consistent and progressive increase in backcalculated lengths at each annulus beginning with the 1979 year-class and proceeding back to the 1976 year-class (Table 2). For example, the length at annulus I for fish caught in 1980 was 23.5, 25.5, 27.2, and 29.2 cm for the 1979, 1978, 1977, and 1976 year-classes, respectively. This pattern is also evident for lengths at annulus II and III (Table 2). Backcalculated lengths at annulus I ranged from 21.9 to 29.2 cm (Table 2), but the observed lengths for 0^+ bass at the end of their first growing season ranged from 7.5 to 29.3 cm ($\bar{x}$ = 16.1 cm, Fig. 1A). The average size of 0^+ bass shifted from 16.1 cm in early December 1980 at the end of the growing season to 22.9 cm in the early spring of 1981 (April) prior to annulus formation (Fig. 1B).

Digestion and Consumption

The time required for 95% digestion decreased as temperature increased (Fig. 2). Digestion rate of shad was not significantly different from digestion rate of minnows at 26°C ($P > 0.10$), but at 20°C digestion rate of minnows was slightly faster ($0.10 > P > 0.05$) than shad. This small difference in digestion at 20° was assumed to have no effect on the final consumption estimates given all the other sources of inherent errors that might be involved in estimating consumption of fish in the field such as effects of meal size and type, predator size, and frequency of feeding on digestion rate (Swenson and Smith 1973). Digestion rate was a linear function of time at each temperature (excluding the residual

TABLE 1. Annual growth, consumption, and gross growth efficiency (K_1) of each major age-class of largemouth bass in Watts Bar Reservoir in 1979 and 1980.

Year caught/ age-class	Mean length (cm) + SD		Mean weight (g)		No. fish	Mean weight over year(g)[b]	Annual weight gain(g)	Weight-specific caloric content (cal/g)	Total caloric gain (cal/g)[c]	Consumption (cal/g)	K_1
	Initial[a]	Final[a]	Initial	Final							
1979											
I^+	23.1±1.9	26.8±3.1	187.6	245.0	42	216.3	57.4	1,140	302.5	1526	0.20
II^+	29.9±2.3	35.6±2.1	422.0	677.8	71	549.9	255.8	1,180	547.8	2743	0.20
III^+	35.9±3.2	43.2±2.2	758.5	1352.7	53	1055.6	594.2	1,390	783.0	4738	0.17
1980											
I^+	23.0±1.5	30.8±3.3	153.4	438.8	63	296.1	285.4	1,100	1060.2	4780	0.22
II^+	31.4±3.6	38.9±2.8	448.6	962.7	118	705.7	514.1	1,280	937.8	4754	0.20
III^+	38.5±3.3	45.9±1.8	902.7	1675.3	72	1289.0	772.6	1,370	821.1	5015	0.16
IV^+	45.9±2.5	51.6±2.7	1660.8	2472.4	22	2066.6	811.6	1,430	561.6	4917	0.11

[a]Initial = start of growing season, final = end of growing season.
[b]Linear growth between monthly measurements assumed.
[c]Calculated as weight-specific caloric content × weight gain/mean weight.

TABLE 2. Backcalculated length at each annulus for the 1976–79 year-classes of largemouth bass in Watts Bar Reservoir.

Year-class/ year caught	Age when caught (yr)	No. fish	Total length, cm (± SD), at annulus			
			1	2	3	4
1976						
1979	3	16	28.6(3.1)	36.2(2.9)	40.1(2.9)	
1980	4	22	29.2(3.3)	37.3(2.0)	43.3(1.7)	46.6(2.2)
1977						
1979	2	51	25.4(3.1)	31.2(3.2)		
1980	3	75	27.2(3.2)	34.8(2.8)	39.0(3.2)	
1978						
1979	1	45	21.9(2.3)			
1980	2	121	25.5(3.0)	31.8(3.2)		
1979						
1980	1	54	23.5(3.1)			

phase), while time to 95% digestion was an exponential function of temperature (Fig. 2) as found for other predators such as pike (Diana 1979), walleye, and sauger (Swenson and Smith 1973).

An average individual of age-class I^+ and II^+ consumed 62 and 42% fewer calories, respectively, in 1979 than in 1980, while consumption of age III^+ was about equal both years (Table 1). Even though consumption of all prey was less in 1979, temporal consumption patterns were similar (Fig. 3). Gizzard shad dominated the diet both years, particularly in the spring before the smaller threadfin were available. In both years, feeding on threadfin shad increased in late spring when spawning shad were congregating in coves, and in the fall when 0^+ threadfin became available. Young threadfin shad dominated the diet of bass in the fall of 1980 (Fig. 3), while in the preceding fall, intake of all prey was low. Alternative prey such as bluegill (*Lepomis macrochirus*) and freshwater drum (*Aplodinotus grunniens*) contributed only 15% of the total energy intake until the summer and early fall of both years when they made up 20–25% of the total.

Size of ingested prey varied between years and seasons. Ages I^+ and IV^+ bass ingested similar-sized prey both years, while ages II^+ and III^+ consumed larger prey in 1980 (Table 3). In the winter–spring periods large shad (15.0–17.5 cm) made up 35% of the diet in 1979 and only 26% in 1980. During the summer of 1979, 37% of the diet were the intermediate 12.0- to 15.0-cm shad, while in 1980 this group contributed only 20% of the diet. Young (0^+) threadfin shad (5–10.0 cm) were important in the diet only during the fall of both years. The reduced consumption by the bass population in 1979 is reflected in a higher percentage of empty stomachs, a lower number of shad per bass stomach, and ingestion of smaller prey by the II^+ and III^+ age-classes (Table 3).

PREY AVAILABILITY

The amount of energy consumed is influenced by prey availability where availability is expressed as abundance and

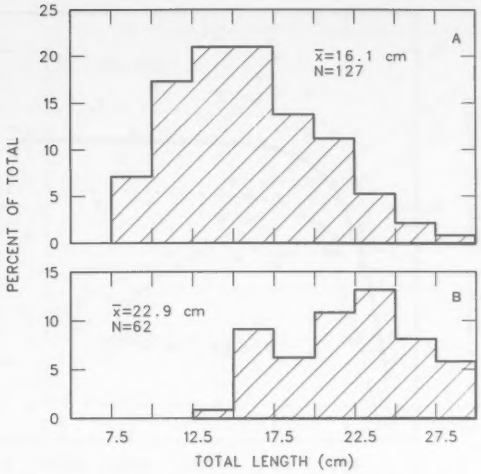

FIG. 1. Shift in length–frequency (2.5-cm size groups) of the 0+ largemouth bass collected in December 1980 at the end of the growing season (A) and in the early spring of 1981 prior to annulus formation (B).

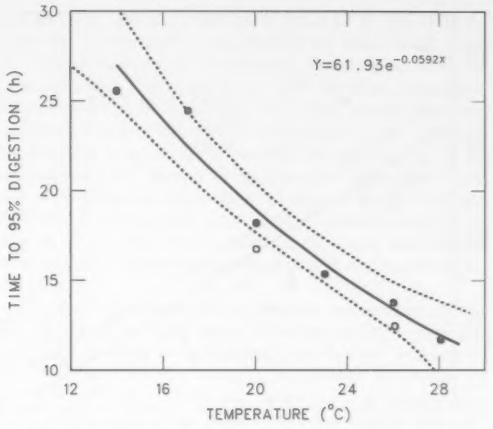

FIG. 2. Relationship between time to 95% digestion (h) and temperature for largemouth bass fed shad (open circles) and minnows (closed circles). The 95% confidence limits for the regression curve are shown.

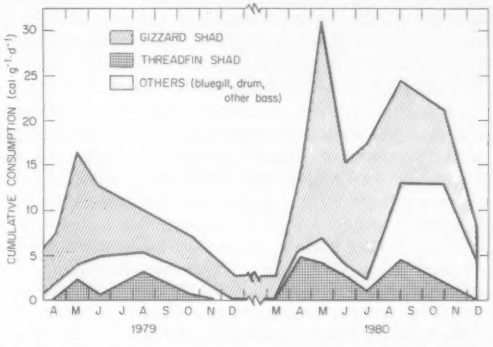
GIZZARD SHAD
THREADFIN SHAD
OTHERS (bluegill, drum, other bass)
CUMULATIVE CONSUMPTION (cal g⁻¹ d⁻¹)
A M J J A S O N D M A M J J A S O N D
1979
1980

FIG. 3. Temporal consumption of prey by largemouth bass in Watts Bar Reservoir over two growing seasons.

size distribution. Relative abundance of prey was inferred from predator food habits and seasonal temperature structure of the reservoir, while size structure of the shad population in the reservoir was reflected by gill net and impingement data. The distribution of shad sizes captured in the gill nets and ingested by bass were similar each season. Ingested prey size, therefore, reflects size availability in the reservoir.

Sizes of prey available to bass in the late winter and spring appear to depend on minimum winter water temperature (Fig. 4). Threadfin shad and small gizzard shad are stressed by cold and become disoriented around 9°C (Griffith 1978). When shad become cold-stressed or die they can become impinged on the screens of water-intake structures such as power plants (McLean et al. 1980). The size distribution and numbers of shad impinged at different temperatures give a

TABLE 3. Mean length (± SD) and weight of prey ingested by each age-class of largemouth bass and feeding data for all age-classes combined during 1979 and 1980 in Watts Bar Reservoir.

Year caught/ age-class	Mean length of ingested prey (cm ± SD)	Mean wt. of ingested prey (g)	% empty stomachs	Mean no. shad/bass	Mean no. prey/bass	Consumption ($mg \cdot g^{-1} \cdot d^{-1}$)
1979						
I+	8.4±2.1	6.2				
II+	10.2±3.1	9.0				
III+	14.7±3.5	27.1				
IV+	16.9±5.1	41.3				
I+–IV+			65	0.37	0.47	0.88
1980						
I+	8.3±2.2	6.0				
II+	13.4±2.7	20.5				
III+	15.6±2.8	32.5				
IV+	16.5±4.0	38.4				
I+–IV+			54	0.56	0.65	1.70

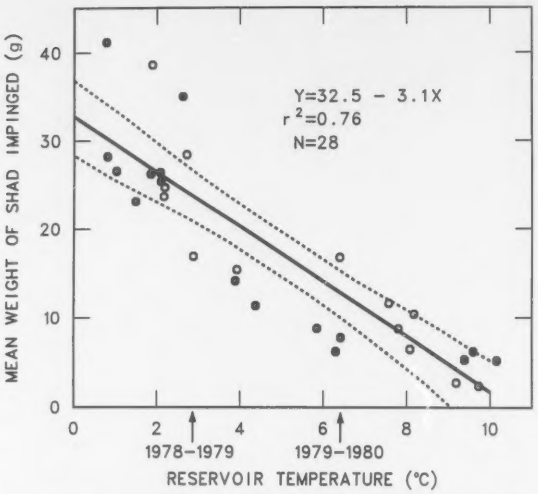

FIG. 4. Relationship of reservoir temperature and average weight of a shad impinged on the intake screens of Kingston Steam Plant during the winter of 1976–77 (closed circles) and the winter of 1977–78 (open circles). Arrows indicate weekly average minimum water temperatures in the winter of 1978–79 and 1979–80. The 95% confidence limits of the regression are shown.

relative indication of the sizes removed by cold kills and the relative magnitude of cold kills on the shad population in the entire reservoir (McLean et al. 1980). A regression of mean weight of shad impinged against reservoir temperature indicated that a linear ($r^2 = 0.76$) was better than a nonlinear fit ($r^2 = 0.73$). The average size of shad stressed by low temperature increased as water temperature decreased, with larger shad killed mainly below 3°C (Fig. 4). In the winter of 1978–79, the lowest weekly minimum temperature was 2.9°C, and only those shad larger than 23.5 g (13.3 cm) probably survived. In the relatively mild winter of 1979–80, the lowest weekly average temperature was 6.4°C, and most shad larger than 12.6 g (10.7 cm) should have survived the winter (Fig. 4).

PREDATOR CONDITION

The visceral–somatic index (% body weight as viscera) and weight-specific caloric content of the viscera were dependent on largemouth bass size (Fig. 5, 6). As predator size increased, the visceral–somatic index increased rapidly, then leveled off (Fig. 5). Viscera weights in the fall tended to be higher than in the spring, especially for those bass on the right side of the inflection point in Fig. 5. In both seasons, the inflection point was about 700 g which approximates the size of an average age II$^+$ bass. The weight-specific caloric content of the viscera also increased with bass size, indicating that larger fish have relatively higher lipid stores in the viscera (Fig. 6). Age-class I$^+$ had significantly lower ($P < 0.05$) viscera weights each season, while differences between the other ages were not significant.

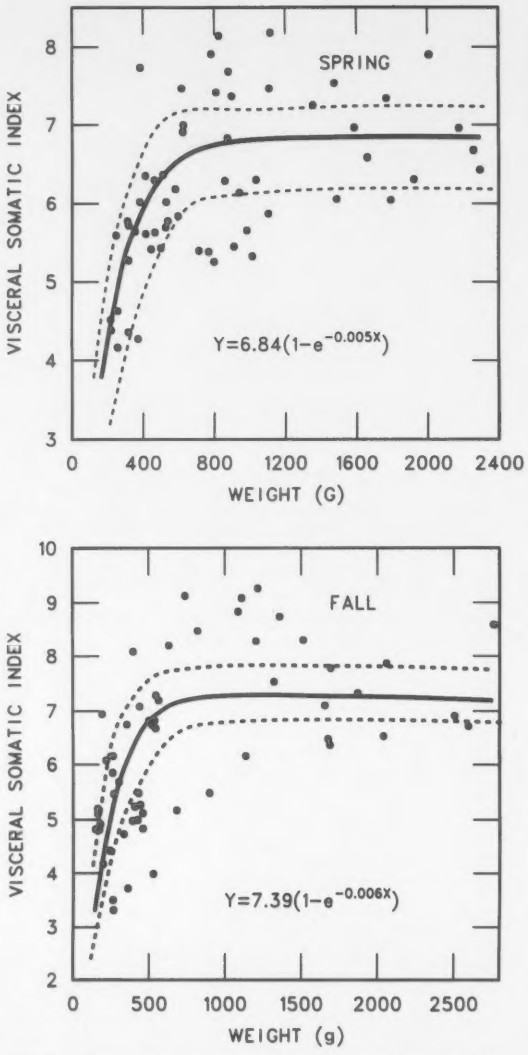

FIG. 5. Relationship between percent of largemouth body weight as viscera and total bass weight during the spring and fall of 1980 with 95% confidence limits of the regression.

Discussion

Relatively small differences in winter water temperature between years (2.9°C vs. 6.4°C) could result in major effects on predator populations. These effects may occur as a result of the threshold relationship between temperature and the lower thermal lethal limits of prey. Field measurements of consumption allowed us to establish the relationship between prey availability and predator growth and mortality.

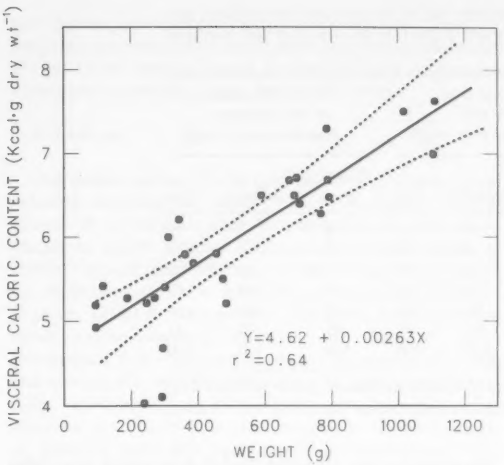

FIG. 6. Relationship between weight of largemouth bass caught during all seasons and caloric content of viscera. The 95% confidence limits of the regression line are shown.

CONSUMPTION AND GROWTH

The consumption methodology developed in this study is designed for warmwater predators that feed at least once a day. The field consumption models of Diana (1979) for northern pike (*Esox lucius*), Popova and Sytina (1977) for pikeperch (*Stizostedion lucioperca*), and Swenson and Smith (1973) for walleye are designed for cold-water species that generally feed less than once a day and have digestion rates longer than 1 d. The consumption methodology appears to produce realistic estimates of daily ration that resulted in gross conversion efficiencies (K_1) ranging from 0.22 for age I^+ bass to 0.11 for age IV^+ (Table 1). This trend of decreasing conversion ratios with increasing age appears reasonable and is consistent with field and laboratory values (6–29%) for predators of similar sizes and life styles (Backiel 1971; Swenson and Smith 1973; Minton et al. 1981; Niimi 1981). Also, three separate estimates of consumption taken 1 wk apart in May 1980 yielded daily ration values of 29.5, 31.1, and 32.5 $cal \cdot g^{-1} \cdot d^{-1}$, suggesting replicability of the method.

Reduced consumption by the bass population in 1979 was probably related to low abundance of all shad smaller than 13.3 cm, particularly in the late winter and spring. Lower consumption rate, larger number of empty stomachs, and smaller number of shad and other prey per bass stomach during 1979 indicate that prey abundance was probably lower that year. Swenson (1977) found that consumption rates of prey in northern lakes were highly correlated with density of prey. Lewis et al. (1974) suggested that percentage of empty stomachs might be a means of evaluating the availability of forage in lakes, and Zweiacker and Summerfelt (1973) found an inverse relationship between percent empty stomachs and growth for largemouth bass.

Low water temperatures in early 1979 (<5°C) reduced the abundance of those shad small enough to be consumed by age I^+ bass (<30 cm) and small age II^+ bass (<31 cm) (Fig. 4, Table 4). Consequently, consumption by these small-sized bass was depressed until midsummer when smaller prey became available. During the entire 1979 growing season age II^+ bass were also consuming prey much smaller than the maximum size they are capable of ingesting (Table 3), possibly resulting in an energetic penality for ingesting less than optimal size prey (Werner 1979). Growth, consumption, and size of prey ingested were about the same both years for age III^+ bass, indicating sufficient numbers of appropriate-sized prey in 1979. These bass consumed the larger shad which were less affected by the low temperatures during both winters (Fig. 4).

The slight depression in consumption and growth during periods of high prey abundance in the summer can be partially explained in terms of largemouth bass thermal preference. The final thermal preferendum of largemouth is between 25 and 27°C (Coutant 1975) and, when surface temperatures were greater than 27°C (August–mid-September), bass inhabited deeper, cooler water (3–5 m). Shad were observed feeding in the upper parts of the water column during the summer, which might spatially segregate them from bass. Bass demonstrated an increase in ingestion of demersal prey such as freshwater drum during this time (Fig. 3). Bluegill, another alternate prey, contributed less than 10% of the total energy ingested by bass during both summers. The thermal preference of bluegill is also higher than that for bass (Reynolds and Casterlin 1976), which would help explain low consumption of this prey. Sunfish appear to be less vulnerable than shad to predation (Lewis and Helms 1964; Aggus 1973), possibly because of decreased efficiency of prey capture in structures such as brush piles that are inhabited by bluegill (Glass 1971).

MORTALITY AND SURVIVAL

The disappearance of the smaller individuals from the largemouth bass population in Watts Bar Reservoir during the winter was due to either growth or mortality of these small fish. Evidence indicates that largemouth bass in this reservoir do not feed or grow during the winter. First, prey was relatively scarce during the winter for those bass smaller than 20 cm (Table 4, Fig. 4). Only 2% of the total shad captured in gill nets during the winter–spring were small enough (8.3 cm) for 20-cm bass to swallow. Also, only 4 bass of the 48 collected during the winter (mid-December to mid-March) contained prey, and these bass were captured in thermal coves of the reservoir where stream input maintained cove temperatures 3–6°C above the main reservoir (McLean et al. 1980). Second, bass are not active and do not feed or grow in temperatures of 10°C or less (Warden and Lorio 1975; Johnson and Charlton 1960; Keast 1968), and reservoir temperatures were 10°C or less from mid-December to mid-March. Third, the condition factor of bass declined during the winter–spring indicating that bass of a fixed length were losing weight during this time of low metabolism. Adams et al. (1982) reported that an average II^+ female and male largemouth bass in Watts Bar reservoir decreased in weight from 755 to 651 g and from 596 to 551 g, respectively, during the winter. The most convincing evidence supporting no winter growth is that

TABLE 4. Maximum lengths of shad that largemouth bass of various sizes can swallow, and the percentage of these maximum length shad caught in gill nets and found in bass stomachs during 1979.

Bass length (cm)	Maximum length shad bass can ingest (cm)[a]	% of total shad in gill nets ≤ maximum prey length			% of total shad in bass stomachs ≤ maximum prey length		
		Winter–spring	Summer	Fall	Winter–spring	Summer	Fall
15	6.5	0	1	1	0	3	15
20	8.3	2	3	8	1	8	28
25	10.4	5	11	25	7	20	48
30	12.7	15	33	38	33	52	63
35	15.3	76	84	69	73	88	86
40	18.3	85	98	97	95	95	97
45	21.4	100	100	100	100	100	100

[a]Maximum shad lengths based on the relationship of Jenkins and Morais (1976): $y = 0.0141x^2 + 0.166x + 1.0772$, where y = prey size (in.) and x = predator size (in.) (1 in. = 25.4 mm).

no scale growth occurred on any bass from December until mid-April when water temperatures rose above 10°C, and bass were feeding.

Because largemouth bass do not grow during the winter, disappearance of the smaller individuals must be due to selective mortality. The progressive increases in backcalculated lengths (negative Lee's phenomenon) at each annulus with older age-classes (Table 2) indicate that selective mortality and not year-to-year variation in growth are primarily responsible for the distribution of sizes within an age-class. If annual fluctuation in growth affected backcalculated sizes, then this would be reflected in the lack of a consistent pattern of size increases at each annulus with each older age-class (random size distribution instead). Negative Lee's phenomenon "is certain to have been caused by selective mortality of one sort or another" (Ricker 1969).

To survive through the spring stress period of reduced prey availability, the predator must have either adequately sized prey or sufficient energy reserves. Evidence was presented earlier that severity of the winter dictates the sizes of prey available in the spring. Even in relatively mild winters, smaller shad (<9 cm) probably suffer mortality, which significantly reduces the forage base for bass smaller than 20 cm (Table 4). The low viscera somatic index (Fig. 5) and weight-specific caloric content of viscera (Fig. 6) also indicate that these smaller fish store very little fat. Therefore, the combination of low fat stores and no available food in the spring results in overwinter mortality of fish less than 20 cm. Other studies support this conclusion. Oliver et al. (1979) found that small smallmouth bass had less chance of surviving simulated winter temperatures in the laboratory because of the higher metabolic demands of small bass which resulted in an exhaustion of their energy supply. Shuter et al. (1980) also reported a higher rate of winter mortality among small young-of-the-year smallmouth bass because the larger fish had a relatively larger supply of energy reserves. First-year mortality in winter was found by Toneys and Coble (1979) to be higher for smaller largemouth bass than larger bass. In contrast, Saiki and Tash (1978) reported that 25- to 35-cm largemouth bass in a backwater area of the Colorado River starved to death in the spring because threadfin shad in this system were either too small (2–5 cm) or too large (16–19 cm) to be consumed.

Size-selective mortality of smaller individuals in a predator population seems to occur in systems where threadfin and gizzard shad are the primary forage and where these prey experience annual winter die-offs. Age–growth data for largemouth bass in Bull Shoals Reservoir, Arkansas (Bryant and Houser 1971), and for sauger and striped bass in Watts Bar Reservoir (Minton et al. 1981; Higginbotham 1979) indicate selective mortality of smaller fish under a fluctuating prey base. In contrast, bass feeding primarily on a stable prey base of bluegills in an Alabama reservoir (Olmsted 1974) and in a Wisconsin lake (Mraz and Threinen 1955) showed no evidence of size-selective mortality. No size-selective mortality was observed for bass in a California lake where threadfin shad are abundant all year (Von Geldern and Mitchell 1975).

Size-selective mortality results in larger average-sized bass of the same age in the spring compared to the previous fall. For example, the average length of age I^+ bass was 26.8 cm at the end of the 1979 growing season and 31.4 cm the following spring at the time of annulus II formation (Table 1). Only the average size of the 0+ age-class at the end of the growing season can be compared directly to annulus I lengths of bass from other systems, because these young fish have not yet experienced the size bias attributed to winter mortality.

To increase the probability of survival through their first winter, therefore, 0^+ bass in Watts Bar Reservoir must attain 25 ± 5 cm by mid-December. A severe winter would dictate that bass be at the upper end of this range by mid-December to increase their probability of overwinter survival. Young bass that are large enough to switch to a fish diet in early fall consume high-energy threadfin shad, a diet which accelerates their growth and enhances the probability that the bass achieve the critical size (about 25 ± 5 cm) for winter–spring survival. This critical survival size is determined primarily by the size of prey available in the spring; prey availability being dictated by winter water temperature. Thus, the size and abundance of available prey affects the amount of food consumed. Food consumption influences growth and growth in

turn dictates size of prey that can be consumed. Survival, therefore, depends on bass being able to grow large enough by the end of the growing season to store sufficient fat over the winter and to consume large shad in the spring.

IMPLICATIONS

Our studies indicate that in populations of predators where selective mortality of smaller fish is occurring, average growth of a year-class may be overestimated when back-calculated lengths are used. Using backcalculated lengths to estimate growth for preceding year-classes may also result in the erroneous conclusion that average growth has decreased from the oldest to the youngest year-class. This error may result in false inferences concerning the effects of various management practices or environmental alterations on growth and survival of a predator population. This size-selective mortality, which we see as a common but annually variable phenomenon in temperate reservoirs, would prevent development of generally applicable age–growth relationships as some authors have proposed. An understanding, however, of the effects of temperature on both predators and prey can aid in formulating management strategies for increasing predator production. Stroud (1967), in summarizing a symposium on reservoirs, emphasized the need for further knowledge about factors that control the availability and consumption of prey in order that dependable management techniques be developed.

Two management strategies for increasing the production of smaller bass would be possible: (1) increase the number of 0^+ bass that reach the 25-cm critical size by the end of the growing season and (2) increase the availability of small prey in the spring. These strategies might be accomplished by managing the system to increase the vulnerability or standing stock of small prey which would be relatively resistent to cold mortality, such as small bluegill or a threadfin × gizzard shad hybrid (McLean et al. 1980). The carrying capacity of small centrarchids in a system may be increased by providing structural complexity such as brush piles (Cooper and Crowder 1979) that provide attachment space for fish food organisms, thus increasing bluegill production (Pardue 1973). Small centrarchids could be made more available to predators in the winter–early spring stress period by lowering water levels where brush piles and other structures would be exposed, thus increasing the vulnerability of these prey.

Reduced survival of smaller individuals in an age-class has implications for both the species and the ecosystem. A fewer number of individuals in an age-class could result in less intraspecific competition for food and space therefore resulting in higher growth rates of survivors. Also, interspecific competition may be reduced especially between young-of-the-year bass and other species. In an ecosystem such as Watts Reservoir where prey undergo large fluctuations in abundance, decreased survival of smaller predators may result in increased fitness to the population. With overwinter mortality of smaller fish, the ecosystem maintains only those larger fish thus maximizing the reproductive potential of the population.

This study has demonstrated that water temperature is a major factor controlling the structure of a predator population through its differential influence on abundance and size-structure of prey. This seasonally fluctuating prey base decreases the survival and growth of age I^+ and II^+ largemouth bass smaller than 30 cm, regulating the structure of the population by controlling the number and sizes of individuals recruited into the adult segment of the population and influencing population reproductive potential.

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Resting Cysts of the Toxic, Red Tide Dinoflagellate *Gonyaulax excavata* in Bay of Fundy Sediments

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During the winter of 1980–1981 sediment samples were collected from 115 stations throughout the southern Bay of Fundy to determine the distribution and abundance of *Gonyaulax excavata* resting cysts. An improved, semiquantitative method of cyst enumeration was developed for this purpose. Resting cysts of *G. excavata* were widely dispersed in the Bay, occurring both offshore and inshore, including the intertidal zone. The great majority of cysts occurred in a large, extremely rich deposit located offshore in the southwestern Bay of Fundy in a zone of fine brown mud at depths of 80–160 m. The location of this deposit was consistent with hydrographic and sedimentary processes in the Bay. Cyst concentrations ranged from 2000 to 8000 cysts·cm^{-3} wet sediment at many stations in the approximately 2000-km^2 deposit. Mouse bioassay tests of cyst extracts (prepared by sonication or boiling) indicated that the cysts were toxic, containing $2-5 \times 10^{-5}$ μg saxitoxin (STX) equivalent per cyst — the same range as for *G. excavata* motile cells in culture. Results support the view that the wintertime acquisition of *G. excavata* toxins by offshore and inshore molluscan shellfish is caused by ingestion of cysts. Results suggest that the offshore seed bed serves as the primary source of the motile cells which initiate the annual *G. excavata* bloom in the Bay of Fundy.

Key words: cysts, *Gonyaulax excavata*, dinoflagellate blooms, red tide, paralytic shellfish toxins, shellfish toxicity, sediments, Bay of Fundy

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Au cours de l'hiver 1980–81, nous avons prélevé des échantillons de sédiment à 115 stations par tout le sud de la baie de Fundy dans le but de déterminer la distribution et l'abondance de kystes de *Gonyaulax excavata*. À cette fin, une méthode semi-quantitative améliorée de comptage des kystes a été mise au point. On a trouvé des kystes de *G. excavata* largement répartis dans la baie, tant au large que près de la côte, y compris la zone intertidale. La grande majorité des kystes se trouvent en un vaste dépôt, très riche, au large dans la partie sud-ouest de la baie, dans une zone de fine vase brune à des profondeurs de 80 à 160 m. L'emplacement de ce dépôt s'accorde avec les processus hydrographiques et sédimentaires de la région. La concentration des kystes se situe entre 2 000 et 8 000 kystes·cm^{-3} de sédiment humide à de nombreuses stations dans le dépôt, qui mesure 2 000 km^2. Des essais biologiques d'extraits de kystes (préparés par traitement à l'ultrason ou par ébullition) indiquent que les kystes sont toxiques, contenant $2-5 \times 10^{-5}$ μg de saxitoxine (STX) par kyste — la même fourchette que pour les cellules mobiles en culture de *G. excavata*. Ces résultats corroborent la théorie que l'acquisition, en hiver, de toxines de *G. excavata* par des mollusques au large et près de la côte est due à l'ingestion de kystes. Ils donnent également à penser que les lits de kystes sont la source première des cellules mobiles responsables du déclenchement de la floraison annuelle de *G. excavata* dans la baie de Fundy.

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THE toxic, marine dinoflagellate *Gonyaulax excavata* forms annual blooms in the Bay of Fundy, along the New England coast, and in the St. Lawrence River Estuary (Hurst and Yentsch 1981; Prakash et al. 1971; White 1982). The blooms have impact on shellfish and finfish resources. Molluscan shellfish accumulate *G. excavata* toxins while feeding, posing the danger to humans of "paralytic shellfish poisoning" (PSP), a potentially fatal food poisoning (Prakash et al. 1971). Finfish, unlike shellfish, are sensitive to the toxins (White 1981b), and during intense blooms fish kills result from toxin transfer through the food web (White 1977, 1979, 1980a, b, 1981a, b).

Gonyaulax excavata blooms in the Bay of Fundy, which occur sometime between May and September, have been consistently more intense since 1974 than at any time in the preceding 30-yr period. This trend is apparent from the yearly shellfish toxicity records compiled since 1943 by the Fish Inspection Laboratory in Black's Harbour, N.B. (White 1982). In 1976 and 1979 the first recorded herring kills caused by *G. excavata* toxins occurred in the Bay of Fundy (White 1977, 1980a). Further, in August 1980 *G. excavata* red water was first documented in the Bay (A. W. White unpublished data; see Prakash 1963; Prakash et al. 1971). The final evidence in support of bloom intensification, and most important in terms of the shellfish industry, is the unprecedented length of the recent harvesting closures of shellfish areas in the Bay. The major soft-shell clam beds along the southwest coast of New Brunswick have been closed to harvesting continuously from June 1980 until the time of writing of this paper (November 1981) because of high levels of *G. excavata* toxins. For the first time since the shellfish toxicity monitoring program was initiated in 1943, shellfish areas had to remain closed during the winter (1980–81).

Gonyaulax excavata perpetuates itself from one bloom season to the next by forming resting cysts (hypnozygotes). The cysts are deposited in the sediment and overwinter there until temperature cues apparently trigger their excystment (Anderson 1980; Anderson and Morel 1979). Resting cysts of *G. excavata* were not described in detail until a few years ago when a sediment sonication technique was used to remove attached debris from the agglutinous cysts, making them visible with the microscope (Anderson and Wall 1978; Dale 1977, 1979; Wall 1975). Reid (1980) drew attention to the need for *G. excavata* cyst studies in the Bay of Fundy in connection with a tidal power project proposed for this area.

A knowledge of the distribution and abundance of these resting cysts in sediments is important primarily for two reasons. First, cysts appear to be selectively deposited by hydrographic and sedimentary processes in certain locations which serve as "seed beds" for producing motile cells which initiate subsequent blooms (Anderson and Morel 1979; Steidinger 1975; Tyler et al. 1982). Such cyst deposits may contribute to our understanding of the dynamics of dinoflagellate blooms. Second, there is evidence that *G. excavata* resting cysts are themselves toxic (Dale et al. 1978) and thus represent a mechanism by which shellfish may become toxic during non-bloom seasons (Yentsch and Mague 1979). The toxicity of resting cysts of *G. excavata* has been suspected for a number of years because of increased toxin content observed in offshore scallops from the Bay of Fundy during the winter months (Bourne 1965; Jamieson and Chandler unpublished data; Prakash 1967). Thus cyst distribution may be useful as an indicator of areas of potential shellfish toxification and accompanying food web problems (e.g. groundfish intoxication, see White 1981b) during non-bloom periods.

In 1977 and 1978 Lewis et al. (1979) investigated the distribution of *G. excavata* cysts in the Gulf of Maine in a semiquantitative manner and revealed a rich cyst deposit in sediments off the coast of Maine near Monhegan Island. However, until the present report, virtually nothing was known about *G. excavata* cysts in eastern Canada. The pattern of bloom intensification in the Bay of Fundy and red water conditions in August 1980 prompted us to undertake a study during the winter of 1980–81 primarily to determine the distribution and abundance of the cysts in Bay of Fundy sediments. An improved, semiquantitative method of sediment sampling and cyst enumeration was developed for this purpose. We report here results of the cyst survey, and of cyst toxicity and excystment studies. Results are discussed in terms of current and sedimentation patterns, *G. excavata* bloom dynamics, and shellfish resources in the Bay of Fundy.

Materials and Methods

SAMPLING STRATEGY

A broad survey of cyst abundance in the southern Bay of Fundy was conducted during January 1981. Results from these cruises indicated an area rich in cysts, to the east and northeast of Grand Manan Island. This area was sampled more intensively during February 1981. In total, sediment samples were obtained from 115 stations between December 1980 and March 1981 (Fig. 1).

SAMPLE COLLECTION

Sediment was collected with a 0.1-m^2 grab (Hunter and Simpson 1976), lowered gently to the bottom to prevent disturbance of the sediment surface. The grab was returned to the ship slowly to minimize washing of collected sediment. When the grab had been set in its cradle, the covering plate was removed. From a place where the sediment surface appeared undisturbed, a "mini-core" of sediment 4.5 cm in diameter and 2.0 cm deep was removed and the wet sediment was placed in a 100-mL plastic container. At station 87 a deep core (7 cm) was taken from the grab sample. The core of sediment was extruded from the collection tube and seven 1-cm-deep sections were sliced off and placed in containers. In all cases the container was immediately capped and the sample was stored in the dark at 2–4°C until analysis. Seawater was not added to the samples. The 13 intertidal samples (stations 103–115) were collected by hand.

LABORATORY ANALYSIS

The entire sediment sample was stirred thoroughly in the plastic container until it appeared homogeneous. In gravelly sediments, rocks and large pieces of shells were scraped clean and removed after homogenization. From this slurry a 1.0-cm^3 subsample was removed by scoop measure and wash-

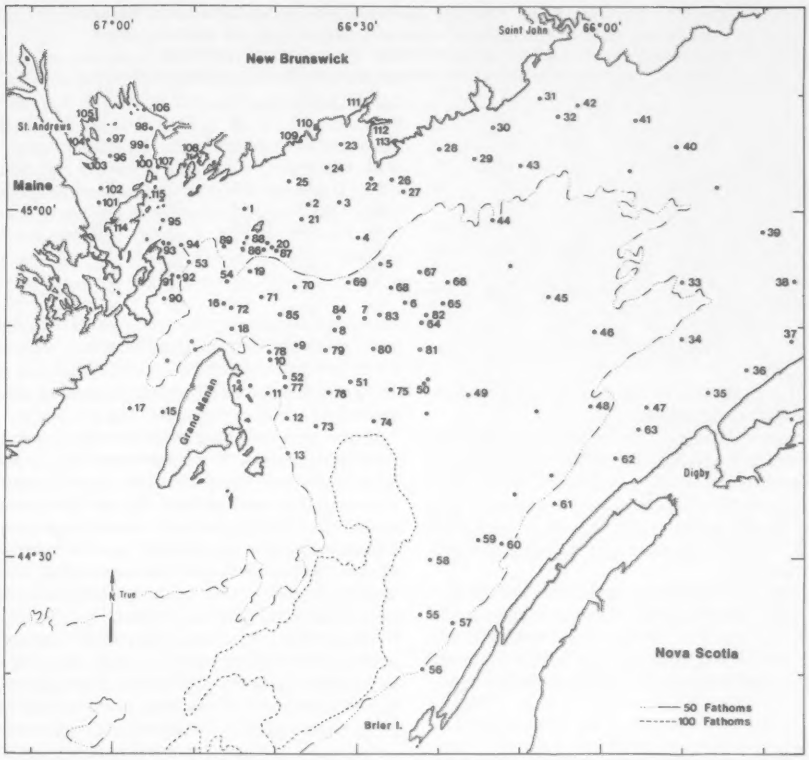

FIG. 1. Locations of sediment sampling stations in the Bay of Fundy area. Sediment samples were not obtained from 12 stations (unnumbered dots) because rocks interfered with operation of the grab. (Note: 50 fathoms ≡ 90m, 100 fathoms ≡ 180 m).

ed with cold filtered seawater into a 15-mL graduated glass centrifuge tube. The subsample was gently sonicated in a Millipore 40-W, 55-kHz cleaning-type water bath for ~1 min. It was then wet-sieved with cold-filtered seawater on a No. 400 (37.5-μm) wire mesh sieve. Because the cysts were about 25 μm in width, some may have passed through the sieve end on, although this possibility was not explored further. Material remaining on the sieve was washed back into the centrifuge tube and centrifuged at 750 × *g* for 5 min.

After centrifugation, the volume in the tube was reduced to 3.0 mL, leaving the cysts in a pellet at the bottom. The subsample was then shaken well and all intact *G. excavata* resting cysts in two or three Palmer–Maloney counting chambers (0.1-mL capacity) were counted. Counts were done on an inverted microscope at a magnification of 150 ×. Mean counts were used to calculate the number of *G. excavata* resting cysts·cm^{-3} wet sediment.

The reproducibility of this method was examined by performing it on nine replicate subsamples from one sediment sample collected on October 31, 1980, from the Bay of Fundy (44°56′N, 66°33′W). Ten Palmer–Maloney counts were made on each subsample.

TOXICITY

The toxin content of *G. excavata* resting cysts from Station 20, collected on January 9, 1981, was determined by two extraction methods on February 6. Toxins were extracted from cysts into acid either by vigorous sonication or by boiling.

By preparatory methods described above, 226 000 cysts were partially purified from the sediment sample. The cysts, now in 3.5 mL of fine sediment, were washed twice with 10 mL of cold 0.1 N HCl by shaking and centrifugation. Then cysts (and sediment) were shaken in 15 mL of 0.1 N HCl and split into two equal subsamples in polycarbonate tubes.

Cysts in one subsample were broken by vigorous sonication (ten 3-min treatments) using a Branson W-350 Sonifier set at "2.5" and fitted with a 1.9-cm horn. The tube was kept in an ice bath during the treatment. Cyst counts showed that 72% of the initial number of cysts had been broken during this procedure. For calculations, it was assumed that all the toxicity of the sonified sample was derived from broken cysts only.

The other subsample was boiled gently for 5 min and cool-

TABLE 1. Replicate, Palmer–Maloney chamber counts of *Gonyaulax excavata* resting cysts (down) made on nine replicate subsamples (across) from one sediment sample processed as described in Materials and Methods. Mean of means equals 63.9.

	1	2	3	4	5	6	7	8	9
	45	56	57	44	72	65	50	81	61
	84	54	84	51	48	78	40	78	65
	67	60	67	75	65	66	40	47	76
	60	53	79	74	69	64	65	65	59
	65	74	71	73	73	50	54	75	81
	64	75	77	50	67	56	63	71	66
	39	56	64	62	63	70	57	69	67
	66	80	87	65	80	66	41	69	73
	37	53	84	54	59	66	51	74	61
	67	62	64	49	74	65	62	69	59
Mean	59.9	62.3	73.4	59.7	67.0	64.6	52.3	69.8	66.8

ed on ice. Boiled cysts were not broken, but their contents appeared bleached and disintegrated.

The acid extracts were adjusted to pH 3.5 with a few drops of NaOH and sent to the Department of National Health and Welfare in Ottawa for mouse bioassay (AOAC 1975). Three mice were tested with the sonicated extract, five mice with the boiled extract. Results are expressed in units of microgram saxitoxin (STX) equivalent because the bioassay is standardized with purified STX.

The toxin content of cysts from station 81, collected on February 10, 1981, was determined after extraction by the boiling method on March 5. Toxins were extracted from 82 000 *G. excavata* resting cysts, partially purified from the sediment sample, and processed as described above.

EXCYSTMENT

The ability of *G. excavata* resting cysts to excyst was followed through the winter months. A known number of resting cysts was placed by micropipette in the base plate of an inverted microscope counting chamber in filtered seawater. The chamber was kept at 11°C on a 14:10-h LD cycle at 2.5 klx from cool-white fluorescent lamps. The numbers of intact cysts and empty thecae were determined daily for 4 d. Cysts still intact after this time were considered incapable of excysting.

Results and Discussion

CYST QUANTIFICATION

The agreement between cyst numbers determined for replicate subsamples of the same sediment sample (Table 1, mean values) indicates that the method used is satisfactory for field survey purposes. Although statistical analysis (one-way ANOVA and Duncan's multiple range test) reveal some inhomogeneity in cyst distribution within the stirred sample, the range of mean values extends only from 18% less to 15% greater than the mean of means. Thus, for practical purposes, cyst concentrations reported in this study are probably subject to less than 25% error.

The method makes a substantial improvement in the comparability of cyst numbers from one location to another over the previously used semiquantitative technique (Lewis et al. 1979) which involved subjective estimates of subsample size, amount of material sonicated, and the amount of material (subsubsample) removed from the settling tube for the final counting operation. In the present method, samples are collected and treated identically. The original sample is a core of known surface area and depth. Its homogenization by stirring ensures that cyst enumeration is conducted on a subsample representative (or very nearly so, see Table 1) of the original sample. Subsampling and sub-subsampling techniques are uniform. Quantification can be made by volume of sediment, as reported here, or by dry weight.

The method is best suited for muddy sediment types. It is not easily (or reliably) used in sandy or gravelly sediments mainly because of the difficulty in obtaining the initial samples in an undisturbed condition. However, the method, combined with viability estimates from excystment studies, should serve as a useful tool for furthering our knowledge of cyst distribution and its role in dinoflagellate bloom dynamics.

An important question is how deep in the sediment cysts can occur, yet still pose an excystment threat. Sediment disturbing processes (such as biological reworking, scouring by bottom currents and by tidal and storm surge, and fishing activities) could expose buried cysts. Generally, studies of *G. excavata* cysts have, as here, focused on sampling the flocculent surface layers of sediment (Anderson and Wall 1978; Dale et al. 1978; Lewis et al. 1979). Yet, results of our one deep sediment core (7 cm) at station 87 showed as many *G. excavata* cysts in the 3- to 4-cm fraction as at the surface, and the presence of cysts to a depth of at least 7 cm. Cyst concentrations for the seven successive 1-cm-deep fractions, from the surface down, were the following: 2080, 870, 860, 2360, 950, 210, and 200 cysts·cm^{-3} wet sediment. The viability of cysts as a function of depth (and age) remains to be determined.

CYST DISTRIBUTION

Gonyaulax excavata resting cysts (Fig. 2) were widely dispersed, occurring in 107 of the 115 sediment samples collected from the southern Bay of Fundy, Passamaquoddy Bay, and the intertidal zone along the southern coast of New Brunswick (Fig. 3, Table 2). Cysts were observed in sediment types

ranging from fine grey and brown mud to sand and gravel (Fig. 4).

The highest concentrations of *G. excavata* resting cysts occurred offshore in the southwestern Bay of Fundy in an area of fine brown mud to the east and north of Grand Manan Island at depths of 80–160 m (Fig. 3, 4). The clustered pattern of very high cyst concentrations indicates an extremely rich cyst deposit in an area covering about 2000 km^2, although patchiness is apparent within the area (Fig. 3). Samples from 13 stations in the area contained 2000–5000 cysts·cm^{-3} wet sediment (Table 2, Fig. 3). Samples from five stations (6, 20, 51, 77, and 81) in the area contained 6000–8000 cysts·cm^{-3} wet sediment (or 7000–12 000 cysts·g^{-1} dry sediment).

For comparative purposes the cyst concentration in a sample obtained from near Monhegan Island off the central coast of Maine in October 1980 was determined. This area in the Gulf of Maine has been described as representing a rich deposit of *G. excavata* cysts (Dale et al. 1978; Lewis et al. 1979). The Monhegan sample contained 3220 cysts·cm^{-3} wet sediment (Table 2, station 116). Thus, based on this one sample, it appears that the Bay of Fundy deposit may be richer in *G. excavata* cysts than the Monhegan deposit.

The lowest concentrations of cysts were found generally in samples collected close to shore or in sandy and gravelly bottom types. Cysts were not observed at six stations in the sand and gravel bottoms along the coast of Nova Scotia, nor at two gravelly intertidal stations in Passamaquoddy Bay near St. Andrews, New Brunswick (Fig. 3). The difficulty in collecting and preparing samples from these kinds of sediments means the results are not a reliable indication of cyst absence. They do, however, reveal a paucity of cysts in these areas. No samples were obtained from 12 stations (unnumbered) because of rocks fouling the grab jaws (Fig. 3).

Cysts were present at most of the intertidal stations along the New Brunswick coast, but at low concentrations (1–499 cysts·cm^{-3} wet sediment, Fig. 3) relative to offshore stations. An exception was Pocologan Harbour (station 110) where 1770 cysts·cm^{-3} wet sediment were found. Interestingly, this has been an area of high shellfish toxicity for many years. Perhaps local hydrographic conditions account for selective deposition of cysts in the area. Lauzier (1967) indicated a shoreward component of residual bottom drift in this vicinity. In any event, the high number of cysts in Pocologan Harbour may explain why shellfish toxicity levels commonly are elevated there, with toxification occurring from the cysts and from subsequent local blooms.

Toxicity

Toxicity tests were positive for both *G. excavata* cyst samples. Cysts from station 20 in January contained 5.0×10^{-5} μg STX equivalent per cyst as extracted by the boiling method, or 4.6×10^{-5} μg STX equivalent per cyst as extracted by the sonication method. These values are not significantly different because the standard bioassay (three-mice test) has a precision of about ±20% (AOAC 1975). Cysts from station 81 in February contained somewhat less toxin, 2.4×10^{-5} μg STX equivalent per cyst (boiling method). Thus the total toxin content of Bay of Fundy cysts appears to be similar to that of the motile cells. The seven strains of *G. excavata* that have been isolated from the Bay of Fundy into culture range in toxin values from 2.2 to 4.5×10^{-5} μg STX equivalent per motile cell (Prakash 1967; White and Maranda 1978; White unpublished data). An isolate of *G. excavata* (No. 429) from Ipswich, Massachusetts, contains between 1.2 and 2.4 μg STX equivalent per motile cell (Alam et al. 1979; Schmidt and Loeblich 1979; White and Maranda 1978).

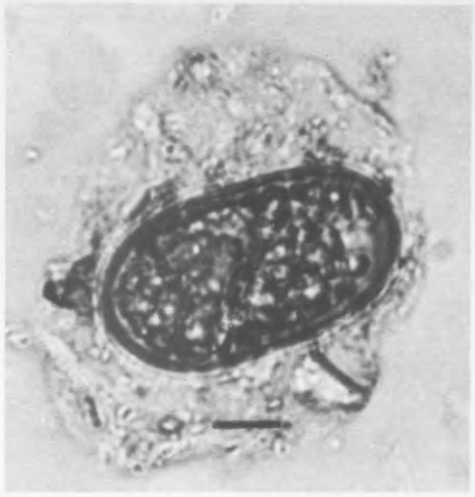

FIG. 2. Typical, ovoid resting cyst (hypnozygote) of *Gonyaulax excavata* showing granular contents and mucilaginous material adhering to the cyst wall. Scale bar equals 10 μm.

There was good agreement between the cyst toxin content values determined by the two extraction methods for the station-20 sample. However, of the two methods, the boiling method is easier and probably quantitatively more reliable. One merely has to prepare, count, add acid to, and boil the cysts. The sonication method is tedious and imprecise, because not all cysts are broken by sonication (72% were broken in this case), cysts must be counted twice, before and after treatment. Further, during sonication, part of the sample is lost because of frothing and intense aerosol formation.

The first and only other record of *G. excavata* resting cyst toxicity was for cysts collected in December 1977 from the deposit near Monhegan Island in the Gulf of Maine (Dale et al. 1978). The cysts were reported to contain about 2×10^{-4} μg STX equivalent per cyst, which is 4–8 times greater than recorded here for Bay of Fundy cysts. Yet this high value may be misleading because it was based on one sample only (split and injected into four mice), and a sonication method was used for toxin extraction. More data are required before conclusions can be reached about possible temporal and spatial differences in toxicity of *G. excavata* cysts, and about the relative toxicity of cysts and motile cells.

Excystment

During January and February 1981, mud temperatures in

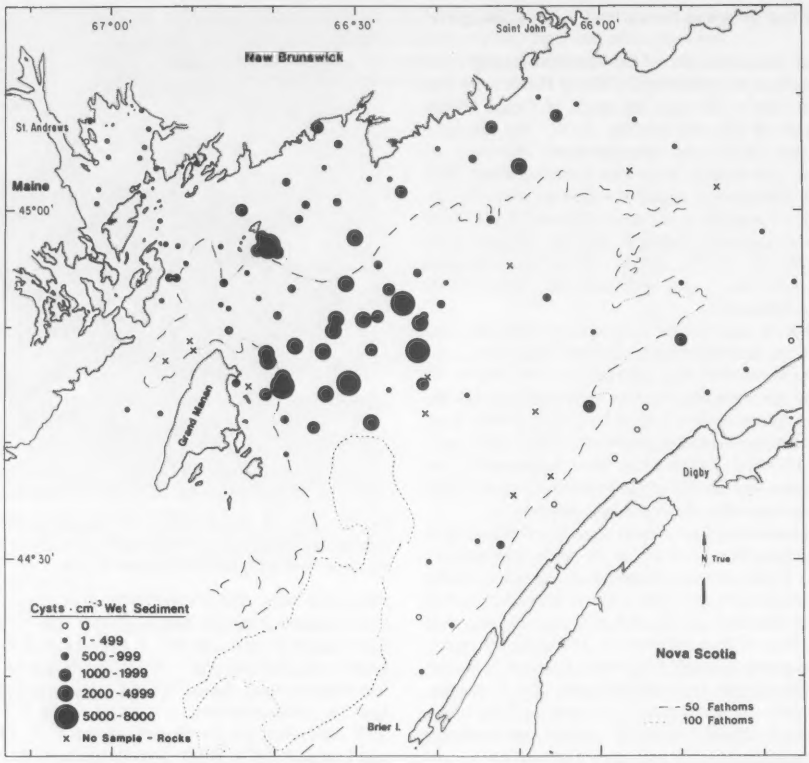

FIG. 3. The concentrations of *Gonyaulax excavata* resting cysts at the sampling stations shown in Fig. 1 during the winter of 1980–81. See Table 2 for details. (Note: 50 fathoms ≡ 90 m, 100 fathoms ≡ 180 m.)

the seed-bed area were 2–3°C and cysts showed no morphological signs of incipient excystment. Only a few empty cysts (cyst walls) were observed in the winter samples. Laboratory, excystment trials during these months showed that only 15–20% of cysts from the seed bed were capable of excystment. But by the end of April 1981, when mud temperatures had reached 5–6°C, cysts throughout the seed-bed area appeared elongated, many with bulbous ends, and with contents undergoing conspicuous Brownian motion not observed in the winter cysts. More empty cysts were observed than in January and February, probably the result of excystment. At this same time, motile *G. excavata* cells were first observed in the surface waters of the southwestern Bay of Fundy, although the water temperature was still too low (5–6°C) to allow rapid vegetative growth. By mid-June, when mud temperatures had reached 7–7.5°C, 30–50% of the cysts observed in the area were empty, and *G. excavata* motile cells had become one of the dominant components of the phytoplankton community.

General Discussion

The expansive and extremely rich deposit of *G. excavata* resting cysts found offshore in the southwestern Bay of Fundy is consistent with, and can be explained by, hydrographic and sedimentary processes within the Bay. The Bay of Fundy is a very dynamic system as a result of pronounced tidal currents associated with the large tidal ranges (5–16 m from mouth to head). Underlying this tremendous tidal flux is a pattern of residual circulation which, together with tidal currents, determines sedimentation dynamics and thus the distribution of *G. excavata* cysts. Encompassing nearly the entire Bay is a counterclockwise residual movement of surface water (Fig. 4; Bumpus and Lauzier 1965; Godin 1968). In the southwestern region there is a counterclockwise gyre of both surface and bottom water, located approximately in the position shown in Fig. 4 (Godin 1968; Lauzier 1967). A large, peninsula-shaped zone of active sediment deposition, caused by relatively low tidal current velocities, occurs in the vicinity of the gyre and to its north, west, and south (Fig. 4; Fader et al. 1977). The surficial sediment type here is predominantly a fine brown mud, described as LaHave clay by Fader et al. (1977). On the other hand, stronger currents in the eastern and central sections of the southern Bay of Fundy scour the bottom and account for large areas of bottom types characterized by sand (Sambro sand) along the coast of Nova Scotia, and glacial till

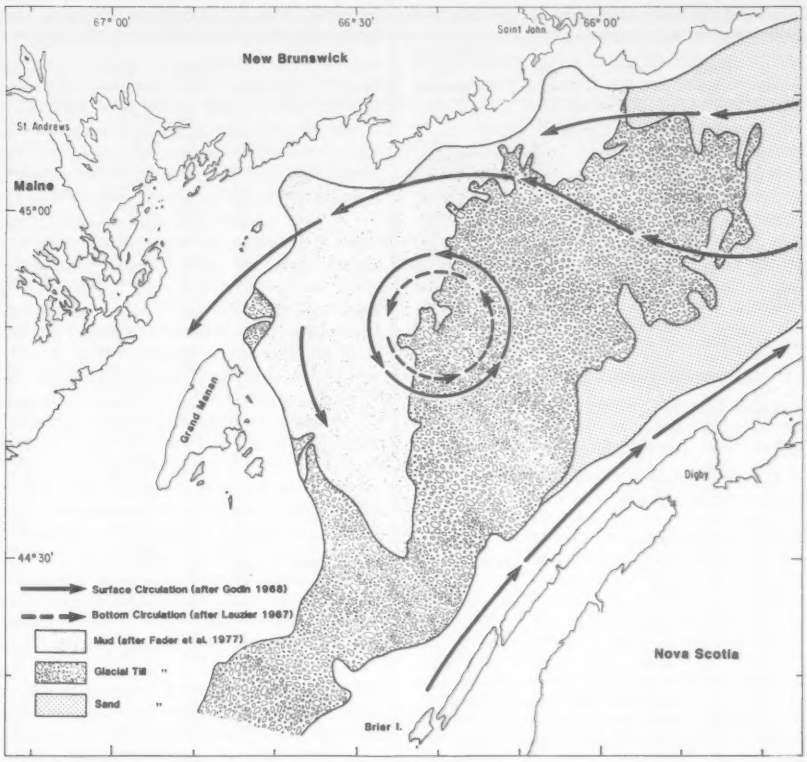

FIG. 4. The pattern of residual circulation of surface and bottom waters in the Bay of Fundy and the distribution of surficial bottom types.

(Scotian Shelf drift) in the central area (Fig. 4; Fader et al. 1977).

The preponderance of *G. excavata* resting cysts occurs in the LaHave clay zone where they are likely deposited by the same mechanism as the silt/clay particles. Cysts are not confined solely to this area, however. Moderate to low numbers of cysts occur nearly throughout the Bay and inshore (Fig. 3). The zone greatly enriched in cysts is very large, covering about 2000 km^2. Cyst deposition in this area may be related to the occurrence of hydrographic fronts. A frontal mechanism has recently been proposed to explain the selective deposition of *Gyrodinium uncatenum* cysts in the Potomac River Estuary (Tyler et al. 1982).

The circulation in the Bay of Fundy must play an important role in returning cysts to, and retaining them in, the southwestern region. In August 1980, during the summer bloom preceding this study, *G. excavata* motile cells were present in large numbers in the southwestern region, but they were also present, although generally in lower concentrations, throughout the remainder of the Bay (White unpublished data). Near the location of station 48 (Fig. 1) in the southeastern area of the Bay, *G. excavata* red water patches occurred, with extremely high numbers of cells (up to 18×10^6 cells/L; White unpublished data). This wide distribution of motile cells in the Bay suggests that newly formed cysts were widely dispersed too. Thus it is likely that circulation processes consolidated the cysts, dispersed throughout the Bay, primarily into the one large site of deposition shown here.

The sheer numbers of cysts in the offshore area suggest that it is this large seed bed, rather than the smaller populations of cysts inshore, that is mainly responsible for producing the motile cells which initiate the annual summer *G. excavata* bloom in the Bay of Fundy. There is evidence, although largely circumstantial, that cysts in the offshore deposit are viable and subject to environmental conditions which enable excystment. The field observations were consistent with Anderson's contention (1980) that *G. excavata* excystment is a temperature-dependent process triggered, after a mandatory resting period of at least several months, when the temperature rises above about 5°C. Little is known about the effects of other environmental factors on dinoflagellate excystment.

The results indicate that Bay of Fundy *G. excavata* cysts are indeed toxic, thus providing strong circumstantial evidence for a mechanism by which molluscan shellfish can acquire *Gonyaulax* toxins during non-bloom seasons. The ingestion

TABLE 2. Summary of *Gonyaulax excavata* resting cyst data for sampling stations in the Bay of Fundy area during the winter of 1980–81.

Date	Stn.	Depth (m)	Cysts · 0.1 mL^{-1}	$\bar{x}$ cysts · 0.1 mL^{-1}[a]	Cysts · cm^{-3} wet sediment
			Bay of Fundy		
Jan. 6, 1981	1	60	23,37,42	34	1020
"	2	50	28,27,27	27	820
"	3	60	24,36,32	31	920
"	4	70	88,103,78	90	2690
"	5	100	20,31,29	27	800
"	6	120	248,268	258	7740
"	7	120	145,136,100	127	3810
"	8	120	68,86,86	80	2400
"	9	120	135,140,144	140	4190
"	10	80	95,113,116	111	3340
"	11	90	36,48,47	44	1310
"	12	110	22,20,18	20	600
"	13	80	1,1,1	1	30
"	14	30	17,22,24	21	630
Jan. 9, 1981	15	80	6,4,5	5	150
"	16	110	0,1,6	2	70
"	17	90	6,6,6	6	180
"	18	150	19,16,17	17	520
"	19	100	3,6,6	5	150
"	20	80	203,188	196	5870
"	21	60	22,28,22	24	720
"	22	30	1,2,1	1	40
"	23	20	19,28,13	20	600
"	24	30	9,14,11	11	340
"	25	50	30,21,28	30	890
Jan. 14, 1981	26	50	1,0,1	1	20
"	27	100	44,46,42	44	1320
"	28	50	10,14,8	11	320
"	29	60	42,28,20	30	900
"	30	50	44,44	44	1320
"	31	30	4,2,3	3	90
"	32	50	42,32,38	37	1120
"	33	90	3,10,12	8	250
"	34	90	38,24,40	34	1020
"	35	90	2,0,0	1	20
Jan. 15, 1981	36	60	1,0,1	1	20
"	37	60	0,0,0	0	0
"	38	80	6,10,6	7	220
"	39	90	0,1,0	1	10
"	40	90	3,1,2	2	60
"	41	60	8,6,7	7	210
"	42	50	18,11,16	15	450
"	43	90	78,96,59	78	2330
"	44	100	36,28,30	31	910
"	45	110	24,24,18	22	660
"	46	100	10,18,10	13	380
"	47	70	0,0,0	0	0
"	48	100	35,53,38	42	1260
"	49	130	4,2,2	3	80
"	50	140	58,69,67	65	1940
"	51	160	227,269	248	7440
"	52	110	97,75,88	87	2600
Jan. 19, 1981	53	90	14,8,11	11	330
"	54	130	10,18,22	17	500
Jan. 21, 1981	55	180	0,0,0	0	0
"	56	90	1,0,0	1	10
"	57	120	8,6,6	7	200
"	58	150	8,12,9	10	290
"	59	130	5,5,5	5	150
"	60	110	18,26,32	25	760
"	61	90	0,0,0	0	0
"	62	100	0,0,0	0	0
"	63	100	0,0,0	0	0
Jan. 22, 1981	64	140	69,122,116	102	3070
"	65	120	32,18,25	25	750
"	66	120	12,14,10	12	360
"	67	120	24,32,26	27	820
"	68	120	52,48,53	51	1530
"	69	100	85,92,104	94	2810
"	70	110	18,18,24	20	600
"	71	80	1,1	1	30
Feb. 9, 1981	72	160	13,8,10	10	310
Feb. 10, 1981	73	150	43,44,38	42	1250
"	74	180	83,70,69	74	2220
"	75	160	12,8,10	10	300
"	76	150	53,62,95	70	2100
"	77	100	171,166	169	5060
"	78	100	73,72,73	73	2180
"	79	120	108,114	111	3330
"	80	160	36,62,42	47	1400
"	81	140	216,249	233	6980
"	82	130	17,17	17	510
"	83	130	58,46,51	52	1550
"	84	120	103,90	97	2900
"	85	110	19,19	19	570
Feb. 13, 1981	86	80	44,28,30	34	1020
"	87	80	56,36,48	47	1400
"	88	80	34,34	34	1020
"	89	80	14,13,16	14	430
Dec. 2, 1980	90	90	2,10,7	6	190
"	91	100	24,20,30	21	630
"	92	100	18,24,17	20	590
"	93	100	11,7,9	9	270
"	94	130	8,12,17	12	370
"	95	70	11,11,13	12	350
			Passamaquoddy Bay		
Feb. 24, 1981	96	40	12,9,10	10	310
"	97	40	7,10,7	8	240
"	98	10	3,2,2	2	70
"	99	30	1,0,1	1	20
"	100	80	4,3,5	4	120
"	101	40	14,16,16	15	460
"	102	30	15,15,15	15	450
			Intertidal — Southwest New Brunswick[b]		
Feb. 28, 1981	103	–	0,0,0	0	0
"	104	–	0,0,0	0	0
"	105	–	1,0,2	1	40
"	106	–	4,5,3	4	120
March 2, 1981	107	–	5,4,3	4	120
"	108	–	5,4,5	5	140
"	109	–	2,6,6	5	140
"	110	–	62,58,57	59	1770
"	111	–	14,6,17	12	370
"	112	–	5,7,6	6	180
"	113	–	11,8,12	10	310
March 11, 1981	114	–	3,8,6	6	170
"	115	–	1,5,4	3	100
			Monhegan Island — Gulf of Maine (43°46'N, 69°19'W)		
Oct. 23, 1980	116	90	78,129,115	107	3220

[a]Values in this column rounded off to nearest whole number.

[b]Locations by name of stations 103–115 are respectively Indian Point, Bar Road, McCann's Cove, Oven Head, Letite, Scotchman's Cove, Crow Harbour, Pocologan, Lepreau Harbour, Lepreau Basin, Dipper Harbour, Northern Harbour, and Stuart Cove.

of cysts (resuspended in the water as a result of tidal or wave action, fishing activities, or shell flapping in the case of scallops) by shellfish has previously been invoked as a possible cause of winter shellfish toxicity (Bourne 1965; Prakash

1967), and more recently as a probable cause (Yentsch and Mague 1979). It explains the rises in toxin level observed in Bay of Fundy scallops during the winters of 1963–64 and 1964–65 (Bourne 1965) and again in 1977–78 and 1978–79 (Jamieson and Chandler unpublished data). It also helps to explain why soft-shell clams (*Mya arenaria*) along the southwestern coast of New Brunswick contained moderately high levels of toxins during the winter months of 1980–81 (generally in the range of 100–500 μg toxins/100 g tissue), necessitating large-scale closures of shellfish areas.

Scallops (*Placopecten magellanicus*) represent a major commercial fishery in the Bay of Fundy. The largest scallop beds lie along the coast of Nova Scotia and extend nearly halfway across the Bay (Caddy 1979). Although great numbers of cysts were not found in this zone of sandy and gravelly bottom types (Fig. 3, 4), there would appear to be sufficient so that ingestion of them by scallops keeps their viscera dangerously toxic year-round (Bourne 1965; Hsu et al. 1979; Jamieson and Chandler unpublished data), excluding all but the adductor muscle[2] from use as food. In March 1978, scallops in this area acquired enormous amounts of toxins (150 000 μg/100 g digestive gland; Jamieson and Chandler unpublished data), most likely from ingestion of cysts. At this level, the scallops may well be lethal to groundfish predators (White 1981b). Scallops in other locations in the Bay of Fundy are contaminated in this same manner, although stocks in the Bay of Fundy proper become more toxic than in Passamaquoddy Bay (Bourne 1965; Jamieson and Chandler unpublished data), which is consistent with the cyst distribution shown here.

Cysts deposited inshore are important because of their impact on the utilization of soft-shell clam resources. Aside from toxin retention after the intense, late-summer bloom in 1980, ingestion of resuspended cysts is the only other tenable explanation of the high toxin levels in clams along the southwestern coast of New Brunswick during the winter of 1980–81. In this case, there was a general pattern either of stability or of slow, progressive decrease in clam toxin contents from the fall through the winter period. Thus it is difficult to know whether wintertime cyst ingestion or retention of the late-summer toxin load was the main cause of the problem. In certain instances, however, substantial rises in clam toxin contents occurred suddenly during the winter period, pointing to the acquisition of toxins from ingestion of cysts.

During the spring, water temperatures rise much more rapidly inshore than offshore, especially in protected shallow coves. Early pulses of excystment of inshore cyst populations and resulting localized *G. excavata* blooms could explain the springtime increases in intertidal shellfish toxicity which have occurred occasionally in some areas in southwestern New Brunswick (White unpublished data) and along the coast of Maine (Hurst and Yentsch 1981). Such spring "mini-blooms" probably would not spread very far from their sites of inception because the temperatures of surrounding waters in April and May are too low to support good vegetative growth. It is not known if motile cells produced early in the year (whether from inshore or offshore cysts) persist in the plankton until temperatures increase and, in this way, contribute to the initiation of the main summer bloom.

In sum, it appears that the offshore area in the southwestern Bay of Fundy serves as the focal point of *G. excavata* cyst deposition. We suspect that this area also serves as the major source of *G. excavata* motile cells which initiate the summer bloom. Under favorable growth conditions, the bloom may propagate from this region throughout the southern Bay, with the resulting cysts being returned to this area for deposition by the prevailing circulation. Hopefully, further study of this seed bed will help in understanding the major aspects of excystment and bloom initiation dynamics in the Bay. Perhaps periodic cyst abundance data from this deposit can be used, along with meteorological and hydrographic data, to help forecast impending contamination, summer or winter, of marine organisms with *G. excavata* toxins.

[2]The scallop adductor muscle remains toxin-free, or very nearly so, year-round.

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A General Theory for Analyzing Catch at Age Data

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FOURNIER, D., AND C. P. ARCHIBALD. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39: 1195–1207.

We present a general theory for analyzing catch at age data for a fishery. This theory seems to be the first to address itself properly to the stochastic nature of the errors in the observed catch at age data. The model developed is very flexible and accommodates itself easily to the inclusion of extra information such as fishing effort data or information about errors in the aging procedure. An example is given to illustrate the use of the model.

Key words: cohort analysis, virtual population analysis, maximum likelihood estimation, aging errors

FOURNIER, D., AND C. P. ARCHIBALD. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39: 1195–1207.

L'article qui suit contient une description d'une théorie générale applicable à l'analyse de données sur les prises par âge dans une pêcherie. Pour la première fois, semble-t-il, cette théorie tient compte de la nature stochastique des erreurs que contiennent ces données. Très flexible, le modèle se prête facilement à l'inclusion de données supplémentaires telles que l'effort de pêche ou des renseignements sur les erreurs dans la détermination de l'âge. L'emploi du modèle est illustré à l'aide d'un exemple.

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THE use of catch at age data for estimating various parameters associated with fish populations dates from the work of Fry (1949), Jones (1964), Gulland (1965), and Pope (1972). These early methods were not stochastic, that is, they did not consider the form of the observational errors which gave rise to the observed catch data or try to extract the additional information which can be gained by analyzing the various cohorts simultaneously. Doubleday (1976) produced a model which dealt with both of these aspects of the problem. Doubleday's approach is somewhat unsatisfactory, however, as a result of the arbitrary nature in which the stochastic element is introduced into the model.

Let C_{ij} be the true catch of age class j fish in year i, and O_{ij} be the estimate of C_{ij} which is to be used in the catch at age model. Doubleday assumes that the variance of the random variable $\log(O_{ij})$ is approximately independent of the value of C_{ij}. In fact, under the most natural assumptions about the stochastic nature of the process which generates the O_{ij}, it would follow that the variance of $\log(O_{ij})$ tends to infinity as the percentage which that age class forms of the catch tends to zero.

Recently Paloheimo (1980) has extended Doubleday's results by including fishing effort information into the estimation procedure. However, the method of introducing the stochastic element into the model remains somewhat unsatisfactory.

The purpose of this paper is to introduce a general model for analyzing a time series of catch at age data for a fishery. When designing such a model, two objectives must be kept in mind. First the model should have the correct stochastic orientation. This means that both the information submitted to the model and the underlying processes which the model describes are subject to error, and that the model should attempt to allocate these errors in a reasonable fashion. Secondly, the model should be flexible; that is, the user should be able to include any information or even opinion which he has into the model and observe its effect on the solution obtained. In the present situation such information could include among other things, fishing effort information, accuracy of aging techniques, accuracy of the estimates of total landings, existence of a stock–recruitment relationship, the effect of environmental factors on recruitment, or changes in size at age of the fish.

The model described here gives methods of combining this information in a systematic way with the catch at age data in order to provide an analysis of the past behavior of an exploited fish population.

The problem of constructing a model for analyzing catch at age data divides itself naturally into three independent parts. First is the assumption of the kind of error structure inherent in the catch at age data and the formulation of the appropriate likelihood function. Second is the adoption of some relationship between the true catches and the instantaneous mortality rates. Finally, there is the assumption of regularities in the instantaneous mortality rates. The analysis of the problem from this point of view leads to a clearer understanding of the role played by each constituent. In addition the resulting model is more flexible in that the structure of any constituent

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can be easily modified if desired without changing the other constituents.

Finally, an important point should be emphasized which is too often overlooked in the design or application of models for analyzing fisheries data. When attempting to apply an existing model to a new set of fisheries data, one almost invariably encounters some new contingency which calls for major or minor revisions of the model. For this reason a model should not be regarded as a final finished product but rather as a flexible framework which can always be modified should the situation require it. We have organized this paper so it follows as closely as possible the actual development of the model. Symbols used are given in the Appendix.

1. The Basic Model

In section 1 the basic model using only catch at age data is developed and the calculations necessary for constructing the computer program are described. This section contains by far the most involved calculations. Once they have been carried out, extra information about the fishery can be incorporated into the model by adding rather simple terms to the log-likelihood function.

In many catch at age analysis models the basic data or set of observations is assumed to be the number of fish caught at each age. It is, in fact, more reasonable to construct a model based on estimates of the total catch (in numbers of fish) and on estimates of the percentage of the catch at each age. This point of view has several advantages for the construction of a stochastic model:

1) There are in fact errors both in estimating total catch and in estimating percentages at age.

2) The errors in estimating the percentages at age have unequal variances and are correlated, and this point of view makes it possible to construct an analytical framework to deal with this situation.

3) It becomes simple to incorporate information about errors in the age estimation procedure into the model.

Let r denote the number of age classes in the fishery and n be the number of years of fishery information. Suppose that in each year i a number of fish are picked out and aged and that S_{ij} are the number of fish observed to be of age j in year i.

Let O_i be the estimated number of fish caught in year i, C_i be the actual number of fish caught in year i, and P_{ij} be the actual percentage of the fish of age j in the catch in year i.

We make the following assumptions:

1) The random variables S_{ij} and O_i are independent.

2) $O_i = C_i \exp(\epsilon_i)$

where the ϵ_i are independent normally distributed random variables with mean 0 and variance σ^2.

3) The S_{ij} are obtained by taking a random sample of the fish and aging it and that there are no errors in the aging procedure.

Given the above stochastic assumptions it follows that the likelihood function for the parameters P_{ij}, C_i, and σ is equal to a constant times

$$1.0 \qquad \prod_{i,j} P_{ij}^{S_{ij}} \prod_i \frac{1}{\sqrt{2\pi}\sigma} \exp\left[-\frac{1}{2}\left(\frac{\log O_i - \log C_i}{\sigma}\right)^2\right].$$

Taking the natural logarithm of 1.0 and ignoring the constant terms, one obtains the log-likelihood function

$$1.1 \qquad \sum_{i,j} S_{ij} \log P_{ij} - \sum_i \frac{1}{2}\left(\frac{\log O_i - \log C_i}{\sigma}\right)^2 - n \log \sigma.$$

Note for later reference that for each i, j the constraints

$$1.2 \qquad \sum_j P_{ij} = 1, \quad P_{ij} > 0$$

hold.

At this point there is no link between the observations S_{ij} and O_i and the underlying process being studied, the exploitation of a fish population. This link is established by the so-called catch equations.

Let F_{ij} and M_{ij} denote the instantaneous fishing mortality and natural mortality for fish from age class j in year i, and N_{ij} denote the number of fish in age class j in year i.

Then we shall assume that the catch equations (Ricker 1975)

$$1.3 \qquad C_{ij} = \frac{F_{ij}}{F_{ij} + M_{ij}} [1 - \exp(-F_{ij} - M_{ij})] N_{ij}$$

$$1.4 \qquad N_{i+1,\,j+1} = \exp(-F_{ij} - M_{ij}) N_{ij}$$

hold.

If the last year class is totally fished out, then equation 1.3 becomes

$$1.3A \qquad C_{ir} = \frac{F_{ir}}{F_{ir} + M_{ir}} N_{ir}$$

1.5 For $1 \le i \le n-1$, $1 \le j \le r-1$, define the quantities Φ_{ij} by

$$\begin{aligned}\Phi_{ij} = {} & \log (F_{ij}) - \log (F_{i+1,\,j+1}) \\ & - \log (F_{ij} + M_{ij}) \\ & + \log (F_{i+1,\,j+1} + M_{i+1,\,j+1}) \\ & + \log [\exp(F_{ij} + M_{ij}) - 1] \\ & - \log [1 - \exp(-F_{i+1,\,j+1} - M_{i+1,\,j+1})].\end{aligned}$$

Equations 1.3 and 1.4 imply that the quantity Φ_{ij} satisfies the equation

$$\begin{aligned}1.6 \qquad \Phi_{ij} &= \log (C_{ij}/C_{i+1,\,j+1}) \\ &= \log (P_{ij}) + \log (C_i) \\ &\quad - \log (P_{i+1,\,j+1}) - \log (C_{i+1}).\end{aligned}$$

If the last age class is totally fished out, then for $j = r-1$ equation 1.5 becomes

$$\begin{aligned}1.5A \qquad \Phi_{i,\,r-1} = {} & \log (F_{i,\,r-1}) - \log (F_{i+1,\,r}) \\ & - \log (F_{i,\,r-1} + M_{i,\,r-1}) \\ & + \log (F_{i+1,\,r} + M_{i+1,\,r}) \\ & + \log [\exp(F_{i,\,r-1} + M_{i,\,r-1}) - 1].\end{aligned}$$

Thus the log-likelihood function for the parameters P_{ij}, C_i, is given by the expression 1.1 subject to the n constraints 1.2 and the $(n-1)(r-1)$ constraints

$$1.7 \quad \log P_{ij} + \log C_i - \log P_{i+1,\,j+1} - \log C_{i+1} = \Phi_{ij}$$

where the quantities Φ_{ij} depend on the instantaneous fishing mortalities F_{ij} and M_{ij}.

If we consider the quantities S_{ij} and O_i to be given, then the expression 1.1 depends on the $nr+n$ quantities P_{ij} and C_i. The maximum likelihood solution to the problem is given by those values of P_{ij} and C_i which maximize 1.1 subject to the $n+(n-1)(r-1)$ constraints 1.2 and 1.7.

This is a large problem and it is impractical to solve it as formulated. However, it is possible to eliminate all the constraints as follows.

Let $\beta_{ij} = \log (P_{ij}C_i/O_i)$

and $\gamma_i = \log (O_i)$.

Then $\log (P_{ij}C_i) = \log (P_{ij}C_i/O_i) + \log (O_i) = \beta_{ij} + \gamma_i$.

Thus the system of constraints 1.7 can be rewritten as

$$1.8 \quad \beta_{ij} + \gamma_i - \beta_{i+1,\,j+1} - \gamma_{i+1} = \Phi_{ij}.$$

Also it is easily verified that

$$[\log (O_i) - \log (C_i)]^2 = \left\{\log \left[\sum_j \exp(\beta_{ij})\right]\right\}^2$$

and

$$P_{ij} = \exp(\beta_{ij}) \Big/ \left[\sum_j \exp(\beta_{ij})\right]$$

so that 1.1 can be rewritten as

$$1.9 \quad \sum_{i,j} S_{ij}\left\{\beta_{ij} - \log \left[\sum_j \exp(\beta_{ij})\right]\right\} - \sum_i \frac{1}{2} \log \left[\sum_j \exp(\beta_{ij})\right]^2 \Big/ \sigma^2 - m \log \sigma.$$

At this stage the $nr+n$ quantities P_{ij}, C_i have been replaced by the nr quantities β_{ij}, and the constraints 1.2 have been eliminated.

In order to eliminate the constraints 1.8, note that it is possible to express any β_{ij} in terms of any other β_{ij} and the Φ_{ij} lying on the same downward sloping diagonal. For example,

$$\beta_{33} = \beta_{11} + \gamma_1 - \gamma_3 - \Phi_{11} - \Phi_{22}.$$

Because there are $n+r-1$ downward sloping diagonals, all the β_{ij} can be expressed in terms of $n+r-1$ of them, the fundamental betas. To decide which betas to use as the fundamental ones, consider the following discussion. When deciding which parameters to employ for parameterizing the likelihood function in a nonlinear parameter estimation problem, it is desirable to employ those parameters which are best determined by the problem and have small covariance with other parameters. The β_{ij} which are best determined are those corresponding to values of i and j for which C_{ij} forms a large proportion of the catch in that year. This will in general occur for a value of j lying about halfway between 1 and r.

Let m be the greatest integer less than or equal to $r/2$. The fundamental betas which have been used are β_{n1}, β_{n2}, . . . , β_{nm}, $\beta_{n-1,\,m}$, . . . , β_{1m}, . . . , β_{1r}.

The problem has now been reformulated as an unconstrained maximization involving the $n+r-1$ fundamental betas and the $(n-1)(r-1)$ quantities Φ_{ij}.

2. Reparameterizing the Instantaneous Mortalities

In section 2 the problem of reparameterizing the instantaneous fishing and natural mortality rates is considered. The purpose of this reparameterization is to enable us to use the model to determine the most regular analysis of the history of the fishery which is consistent with the catch at age data, whereby regular is meant that analysis of the fishery in which the estimates of fishing and natural mortality vary in the simplest biologically meaningful manner.

Up to now the problem has not been solved; it has merely been restated. This is because the $(n-1)(r-1)$ quantities Φ_{ij} depend on $2nr$ quantities, the F_{ij} and M_{ij}, so that the problem now depends on $n+r-1+2nr$ quantities; whereas originally we had just the $nr+r$ quantities P_{ij} and C_i.

The reason why some progress has been made is that the instantaneous mortality rates can be reparameterized to exploit underlying regularities in the process being studied. For example, one can assume, as is often done, that the instantaneous natural mortality rate is independent of year class and fishing year. Then $M_{ij} = M$ and the number of instantaneous natural mortality quantities has been reduced from nr to 1. More complicated schemes of parameterizing the instantaneous natural mortality are possible. For example, one could assume that the instantaneous natural mortality is a linear function of age class so that

$$M_{ij} = a + bj.$$

In the situations studied to date it was discovered that instantaneous natural mortality was not determined sufficiently well to justify attempts to determine age-dependent effects, and age-independent natural mortality has been used throughout. Further research should be done in order to determine whether there are conditions under which finer estimates of natural mortality can be obtained.

The possibilities for parameterizing instantaneous fishing mortality are considerably more varied. In order to get a general idea of how to proceed, we consider that fishing mortality depends on the interaction of two systems, fishermen and fish. If the fishermen do not fish, the fishing mortality will be zero, no matter what the fish do. On the other hand, if a particular year class is too small to be caught, or is in another area, its fishing mortality will be zero no matter what the fishermen do. With these ideas in mind Doubleday (1976) employed a two-factor model $\log (F_{ij}) = a_i + b_j$, where a_i represents a general level of fishing mortality due to the fishermen, and b_j represents the relative level of fishing vulnerability of year class j.

We use here a different approach to parameterizing the instantaneous fishing mortality in addition to Doubleday's method. It was hypothesized that the fishing vulnerability should follow an age-dependent trend and should therefore be estimated by a curve depending on a smaller number of parameters than the number of age classes.

As a first attempt to reparameterize the fishing mortality rate, a parabola was employed. This had the disadvantage that if the fishing vulnerability increased very quickly at the beginning, it must at some point decrease very quickly. To overcome this difficulty we employed a nonlinear rescaling of the j index. The expression for the fishing mortality curve is

$$2.1 \quad \log F_{ij} = b_1 j(s) + b_2 j(s)^2 + a_i$$

where the method for rescaling the j index is given by

$$2.2 \quad j(s) = -1 + 2\,(1 - s^{j-1})/(1 - s^{r-1})$$

with $0 < s < 1$, hereafter referred to as the VB parameterization.

3. The Incorporation of Fishing Effort

In many situations one has not only catch at age information for a fishery but also estimates of fishing effort. There are three reasons for including such information into the model. First, if there is a relationship between fishing effort and fishing mortality which can be modeled, then the time series of effort contains extra information which can be used to improve the estimates of whatever it is one wants to know. Such information improves the estimate of natural mortality. Second, it may be desirable to estimate the relationship, if any, between fishing effort and fishing mortality in order to determine what desirable levels of fishing effort are. In particular it is possible to examine the data for evidence of time-dependent trends in catchability. Finally, if the last year class is not fished out, such information improves estimates of the number of survivors.

In this model it has been assumed that for a given year the average level of instantaneous fishing mortality is related to effort. More precisely, let E_i be the total fishing effort in year i. It is assumed that

$$3.1 \quad \log F_{ij} = b_{ij} + \log (q_i) + \log (E_i) + D_i$$

where $b_{ij} = b_1 j(s) + b_2 j(s)^2$

where in equation 3.1 D_i represents the deviation from the general level of fishing mortality for the year i.

The quantities D_i are assumed to be normally distributed random variables with mean 0 and variance σ_1^2. Thus the sum $\sum_i D_i^2/2\sigma_1^2$ is subtracted from the log-likelihood function.

4. The Problem of Relative Error Sizes

Section 4 treats the problem of estimating the relative magnitude of the errors present in the various types of information used by the model.

As we already stated, a stochastic model should attempt to allocate errors in a reasonable fashion. In this regard consider the assumption that the S_{ij} are obtained by aging a random sample of the catch. Now in most cases the sampling of the catch is almost certainly not random. For example, it is in general not possible to sample the catches from all boats, and in many fisheries the age structure of the catch may differ substantially from boat to boat and season to season. Other problems arise in sampling the catch from a particular boat. At this point then the reader may well wonder about the wisdom of assuming a random sampling scheme in the model. The answer is twofold. First the assumption of a random sample is akin to the assumption of normality made in many situations in that it is in some sense the simplest assumption to make in the absence of further information. To understand the second reason for the suitability of this assumption, consider a random sample of 400 fish from a population which consists of 20% 5-yr-old fish and 1% 10-yr-old fish. The expected numbers of 5- and 10-yr-old fish are 80 and 4 fish. Now an actual turnout of 6 age 10 fish would not be surprising; however, an actual turnout of 120 age 5 fish would be highly unusual. In both cases the percentage error is 50%. Thus the percentage error in estimating a population percentage gets large as the population percentage gets small.

Let p be the true population percentage and $\hat{p}$ be an estimate of p derived from taking a random sample of size m. The variance of $\hat{p}$ is $p(1 - p)/m$, and the variance of $\hat{p}/p$ is $(1 - p)/pm$, which becomes unbounded as p tends to zero.

This seems to be a fundamental property of sampling errors which should hold even when the sampling is not truly random. The adoption of the random sample hypothesis and the use of the corresponding likelihood function ensures that these relative error size probabilities will be respected when the model attempts to fit the data.

Another question raised by these considerations is the problem of sample size. Because of the unknown errors involved it is probably not true that a sample 25 times as large yields 5 times more accurate estimates, which is what sampling theory would predict if the samples were random.

For this reason the sample sizes have been scaled so that they are all equal to 400. This means approximately that if a true population percentage is 0.2, then the observed value would lie between 0.16 and 0.24 96% of the time. Of course if it is known that the age structure data for certain years is bad, the sample sizes for these years can be set correspondingly lower.

Because the age sample sizes have been fixed in a somewhat arbitrary fashion, it was not considered necessary to estimate σ^2, and σ^2 was set to be equal to 0.0025. This corresponds to approximately a 5% average error in estimating the total number of fish caught.

The question of determining the size of σ_1^2 is of a different nature than the determination of stock size and σ^2. This is because one must assume that the age structure and total catch information are relatively accurate, because if it is not, then there is no information, and hence no basis on which to do any analysis. An appropriate procedure is to start with a small value of σ_1^2, observe the resulting relationships, and then increase σ_1^2 if this seems necessary to get a better fit between predicted and observed age structure and total catch data. The effects of this procedure on the original solution can be ob-

served and the appropriate conclusions drawn.

Thus σ^2 and ${\sigma_1}^2$ are not regarded as quantities to be estimated but are held at fixed values. Let $w = 1/\sigma^2$ and $w_1 = 1/{\sigma_1}^2$. With this provision the log-likelihood function is given by

$$4.1 \quad \sum_{i,j} S_{ij}\left\{\beta_{ij} - \left[\log \sum_j \exp(\beta_{ij})\right]\right\} - w \sum_i \frac{1}{2}\log\left[\sum_j \exp(\beta_{ij})\right]^2 - w_1 \sum_i \frac{1}{2} D_i^2.$$

The quantities w and w_1 can be thought of as penalty weights which determine what penalty must be paid for deviating from the observed total catch or the effort-fishing mortality relationship.

These procedures for adjusting the various variances until a suitable fit is deemed to be achieved may seem somewhat arbitrary to the reader, and they are. It is simply an inescapable fact that the age structure and effort data do not contain enough information to determine the relative accuracies of the aging data, the total catch data, the regularity of fishing mortality, or the closeness of the relationship between effort and average fishing mortality. These procedures do, however, give the user a precise quantitative method of exploring the results of various assumptions about the relative error sizes involved.

5. Factors Affecting Recruitment

A serious deficiency in the model as it now stands is its inability to predict what will occur in the fishery in the future. This is because there is no mechanism for predicting future recruitment. If there were such a mechanism, then because there are already estimates of the relationship between fishing effort and fishing mortality, it would be possible to construct scenarios describing the future behavior of the stock under various management strategies.

There are two obvious factors which may affect recruitment: parent stock size and the environment. The environment is of course a catch-all phrase for a host of factors. Whereas environmental factors may be very important in determining recruitment, recruitment relationships based primarily on environmental factors may not be of much value for predicting future stock behavior, as the future value of the factors may be essentially unknowable.

On the other hand knowledge of environmental factors affecting recruitment may be of great importance in order to have the greatest possible lead time for predicting serious recruitment failures so that appropriate action can be taken.

In this section we consider the effects of stock size only on recruitment.

There are many aspects of parent stock condition which may have a bearing on the resulting recruitment. For simplicity we consider only a simple situation. We assume that the recruitment depends on the reproductive potential of the female members of the stock and we have used the "Ricker curve" for the relationship. The reader who does not believe in this form of stock–recruitment relationship should be reassured that it is used only for illustrative purposes and that any other desired relationship could easily be substituted.

Let f_j denote the relative reproductive potential of age class j fish (The f_j could be made time dependent if the information were available and if that were deemed advisable.)

Suppose that the age of recruitment is a. The reproductive potential of P_i of the population in year i is given by

$$5.1 \quad P_i = \sum_j f_j N_{ij}.$$

The stock–recruitment relationship is assumed to have the form

$$5.2 \quad N_{i+a,1} = \alpha P_i \exp(-\delta P_i)\, e^{\epsilon_i}$$

where the ϵ_i are normally distributed random variables with mean 0 and variance ${\sigma_2}^2$. The contribution to the log-likelihood function from the stock–recruitment relationship is

$$5.3 \quad -\sum_{i=1}^{n-a} \frac{1}{2}(\log (N_{i+a,1}/P_i) - \log \alpha + \delta P_i)^2/{\sigma_2}^2.$$

Because the f_j are constants and equation 1.3 can be used to eliminate the N_{ij}, only two new parameters are introduced into the model. (${\sigma_2}^2$ is treated as a constant as discussed in the section on the Problem of Relative Error Sizes.)

6. Errors in Aging

The problem posed by small aging errors in applying the model to certain fish populations cannot be overemphasized. Such populations are those where recruitment varies widely from year to year. To see why this is so, consider an aging procedure which is accurate for the first age class and suppose that for age classes 4, 5, and 6 the procedure gives the correct age 80% of the time and is either one year high or low 10% of the time. Suppose that age classes 4 and 6 are from large cohorts and age class 5 is from a small cohort so that the true age structure of the catch is 60% fours, 5% fives, and 20% sixes. Then with the above assumptions about the aging errors it is easily seen that the expected percentage of age class 5 fish observed will be 12% which would be a 140% error.

When a small cohort is followed through the fishery it would be observed to have abnormally low fishing mortality at the beginning and abnormally high fishing mortality at the end with the result that the true regularities in fishing mortality, whose existence the model is trying to exploit, would be masked. In addition, interpretation of model fit is made more difficult.

Another problem caused by small aging errors is that very large recruitments appear smaller and, (perhaps more serious) very small recruitments appear larger. This effect will make the identification of environmental factors affecting recruitment, especially those leading to catastrophic recruitment failures, more difficult.

A great advantage of this model is the simplicity with which aging error information can be incorporated into it.

Let a_{jk} be the probability that a fish from age class k will be judged to lie in age class j.

The probability that a fish picked at random in year i will be judged to lie in age class j is given by

$$6.1 \quad \sum_k a_{jk} P_{ik}.$$

The first terms in the log-likelihood function become

$$6.2 \quad \sum_{i,j} S_{ij} \log \left(\sum_k a_{jk} P_{ik} \right)$$

while the other terms are unaffected. Because

$$P_{ik} = \exp(\beta_{ik}) \Big/ \sum_l \exp(\beta_{il})$$

the log-likelihood function becomes

$$6.3 \quad \sum_{i,j} S_{ij} \log \left\{ \sum_k a_{jk} \left[\exp(\beta_{ik}) \Big/ \sum_l \exp(\beta_{il}) \right] \right\} - \sum_i \frac{1}{2} \left[\sum_j \exp(\beta_{ij}) \right]^2 \Big/ \sigma^2$$

where the log-likelihood contributions from the fishing effort information and stock–recruitment relationship etc. have been omitted.

7. Grouping the Aging Data for the Older Age Classes

Some species of fish may have so many age classes present in a fishery that it is desirable to group the aging data for older age classes together rather than consider them separately. Aging the older fish may be very time consuming, and in addition the estimates of the ages of the older fish may be so inaccurate that including them will actually degrade the performance of the model. The grouping of the aging data for the older age classes can be accomplished by a simple modification of the likelihood function.

Suppose that the aging data for all fish lying in age classes s to r inclusively are to be grouped. Let

$$7.1 \quad T_i = \sum_{j=s}^{r} S_{ij}.$$

The first part of the log-likelihood function (1.1) becomes

$$7.2 \quad \sum_{i=1}^{n} \sum_{j=1}^{s-1} S_{ij} \log (P_{ij}) + \sum_{i=1}^{n} T_i \left[\log \left(\sum_{k=s}^{r} P_{ik} \right) \right].$$

8. An Example

To illustrate how various aspects of the model function in practice, we simulated an exploited fish population and analyzed the resulting observations using the model. The results are presented here.

The population simulated had a natural mortality rate of 0.5, and a Ricker type of stock–recruitment relationship (expression 5.2) with alpha = 9.0, delta = 0.006, and a variance $\sigma_2^2 = 0.09$.

TABLE 1. The actual number of fish at age.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	400	1000	600	200	300	50	10	20	5	2
2	1000	236	556	304	91	125	19	4	7	2
3	700	595	135	297	151	43	55	8	2	3
4	300	416	339	72	148	70	19	24	3	1
5	67	172	212	143	25	42	17	4	5	1
6	97	39	89	92	51	7	11	4	1	1
7	118	54	17	29	21	9	1	1	0	0
8	241	70	31	9	14	10	4	0	1	0
9	1007	144	40	17	5	7	5	2	0	0
10	301	596	81	21	8	2	3	2	1	0
11	478	169	281	29	6	2	0	0	0	0
12	470	273	84	113	9	1	0	0	0	0
13	378	280	157	46	58	4	1	0	0	0
14	917	207	122	48	9	8	0	0	0	0
15	357	512	96	43	12	2	1	0	0	0
16	861	211	289	50	20	5	1	1	0	0
17	738	512	120	153	25	9	2	0	0	0
18	629	429	271	55	60	8	3	1	0	0
19	465	364	225	122	21	19	2	1	0	0
20	463	276	206	118	59	9	8	1	0	0

TABLE 2. The catch at age.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	8	66	78	39	75	14	3	7	2	1
2	15	11	52	44	17	27	5	1	2	0
3	10	28	13	43	28	9	13	2	0	1
4	13	53	83	25	64	34	10	13	2	0
5	3	20	48	47	10	19	8	2	3	0
6	7	8	33	47	31	5	8	3	1	1
7	2	3	2	4	4	2	0	0	0	0
8	3	3	2	1	2	2	1	0	0	0
9	19	8	5	3	1	2	1	1	0	0
10	18	106	27	10	4	1	2	1	0	0
11	23	24	76	11	3	1	0	0	0	0
12	6	11	7	14	1	0	0	0	0	0
13	30	63	63	25	37	3	0	0	0	0
14	57	38	41	22	5	5	0	0	0	0
15	6	29	11	7	3	0	0	0	0	0
16	14	11	29	8	4	1	0	0	0	0
17	24	51	23	43	9	4	1	0	0	0
18	22	46	56	17	23	4	1	0	0	0
19	8	19	24	20	4	5	1	0	0	0
20	11	21	31	26	17	3	3	0	0	0

TABLE 3. The aging error probabilities.

True age	Underage by 1 yr	Correct age	Overage by 1 yr
4	0.00	0.80	0.20
5	0.10	0.70	0.20
6	0.10	0.65	0.25
7	0.20	0.60	0.20
8	0.25	0.55	0.20
9	0.30	0.50	0.20
10	0.40	0.40	0.20
11	0.40	0.40	0.20
12	0.50	0.40	0.10
13	0.50	0.50	0.00

The fishing mortality was generated according to the VB parameterization described by expression 3.1 with deviations from average fishing mortality having a variance $\sigma_1^2 = 0.09$. The actual fishing mortality is given in Table 5.

The population, catch, and observed age structure of the catch were generated by stochastic simulation. The stochastic element consists of three parts, the stochastic error in the effort-fishing mortality relationship, the stochastic error in the stock–recruitment relationship, and the sampling error in sampling the catch for fish to age. For each year a random sample of 400 fish was generated from the catch and aged according to the aging error probabilities shown in Table 3.

The analysis has been split up into four sets of computer runs of the model. The first set investigates the performance

TABLE 4. The observed numbers at age in the aging samples (from aging 400 fish with aging error probabilities given in Table 3).

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	16	77	113	83	60	33	10	6	2	0
2	28	38	103	108	52	46	17	4	3	1
3	31	68	58	98	63	47	23	10	2	0
4	27	65	80	70	82	40	19	14	3	0
5	11	50	114	96	51	40	26	6	4	2
6	16	24	116	130	70	26	10	7	1	0
7	41	60	61	102	71	40	20	2	3	0
8	73	83	54	53	57	47	13	13	6	1
9	153	127	52	27	15	12	12	2	0	0
10	57	187	87	34	16	9	4	5	1	0
11	61	77	171	74	11	2	1	2	1	0
12	69	84	110	86	41	8	1	0	0	1
13	46	102	105	74	51	22	0	0	0	0
14	117	97	86	66	18	8	8	0	0	0
15	61	152	101	66	16	4	0	0	0	0
16	78	83	124	64	32	12	5	2	0	0
17	56	109	101	91	32	7	4	0	0	0
18	55	96	118	71	31	24	4	1	0	0
19	28	88	117	101	43	14	7	2	0	0
20	38	84	99	96	50	24	4	4	1	0

TABLE 5. The actual fishing mortality.

The relative fishing vulnerability									
0.050	0.159	0.329	0.517	0.686	0.816	0.906	0.964	1.000	1.000

The instantaneous fishing mortality

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	0.03	0.09	0.18	0.28	0.37	0.45	0.49	0.53	0.55	0.55
2	0.02	0.06	0.13	0.20	0.26	0.31	0.35	0.37	0.38	0.38
3	0.02	0.06	0.13	0.20	0.26	0.31	0.35	0.37	0.39	0.39
4	0.06	0.18	0.36	0.57	0.76	0.90	1.00	1.07	1.11	1.11
5	0.05	0.16	0.33	0.52	0.69	0.82	0.91	0.97	1.01	1.01
6	0.09	0.30	0.62	0.98	1.29	1.54	1.71	1.82	1.89	1.89
7	0.02	0.06	0.13	0.20	0.26	0.31	0.35	0.37	0.39	0.39
8	0.02	0.05	0.10	0.16	0.21	0.25	0.28	0.29	0.30	0.30
9	0.02	0.08	0.16	0.25	0.33	0.40	0.44	0.47	0.49	0.49
10	0.08	0.25	0.52	0.83	1.10	1.30	1.45	1.54	1.60	1.60
11	0.06	0.20	0.41	0.65	0.86	1.03	1.14	1.21	1.26	1.26
12	0.02	0.05	0.11	0.17	0.22	0.26	0.29	0.31	0.32	0.32
13	0.10	0.33	0.69	1.08	1.44	1.71	1.90	2.02	2.10	2.10
14	0.08	0.26	0.54	0.86	1.14	1.35	1.50	1.60	1.66	1.66
15	0.02	0.07	0.15	0.24	0.32	0.38	0.42	0.45	0.47	0.47
16	0.02	0.07	0.14	0.21	0.28	0.34	0.38	0.40	0.41	0.41
17	0.04	0.13	0.28	0.44	0.58	0.69	0.77	0.82	0.85	0.85
18	0.05	0.15	0.30	0.48	0.63	0.75	0.83	0.89	0.92	0.92
19	0.02	0.07	0.14	0.23	0.30	0.36	0.40	0.42	0.44	0.44
20	0.03	0.10	0.21	0.33	0.44	0.52	0.58	0.61	0.64	0.64

The actual effort

2	1	1	5	4	5	1	1	2	5
4	1	5	3	1	1	3	2	2	2

The deviations in the effort-fishing mortality relationship

−0.23	0.11	0.11	−0.44	−0.31	0.09	0.11	−0.12	−0.35	−0.08
−0.09	−0.07	0.20	0.47	0.30	0.19	−0.20	0.29	−0.46	−0.08

TABLE 6. The stock−recruitment relationship.

The coefficients for the Ricker curve

$\alpha = 9.0$ $\delta = 0.006$

The age of recruitment is 4.

The relative reproductive potentials

0.10	0.20	0.30	0.50	0.70	0.90	1.00	1.00	1.00	1.00

The maximum reproduction is at 0.57 times the average reproductive potential of 295.

The reproductive potentials (for years 1−16)

812	674	590	464	258	150	67	75	166	197
186	191	209	208	200	260				

The predicted recruitment (without stochastic error for years 5−20))

55	105	153	257	493	549	404	432	551	543
548	546	536	537	542	491				

The stochastic error in the stock−recruitment relationship

0.177	−0.086	−0.268	−0.066	0.713	−0.600	0.167	0.082	−0.378	0.523
−0.429	0.455	0.319	0.158	−0.152	−0.059				

SET 1: This set of runs represents the best analysis of the population which could be obtained from the data. In particular, it is assumed that the aging error probabilities are known and have been supplied to the model. The results from set 1 are summarized in Tables 7 through 10.

TABLE 7. Value of the objective function for different values of the instantaneous natural mortality M.

M	0.3	0.4	0.5	0.6	0.7
Objective function	85.6	84.6	84.2	84.3	85.0

TABLE 8. The estimated number of fish at age.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	365	1024	602	216	227	86	7	4	10	0
2	937	215	567	303	98	94	33	2	1	3
3	647	557	122	302	151	46	41	14	1	1
4	382	384	317	65	149	70	20	17	6	0
5	52	219	193	131	22	41	16	4	3	1
6	97	30	112	83	46	6	11	4	1	1
7	123	53	13	36	19	8	1	1	0	0
8	275	73	30	7	18	9	3	0	0	0
9	1006	165	42	17	4	9	4	2	0	0
10	322	596	93	22	8	2	4	2	1	0
11	456	181	284	35	6	2	0	1	0	0
12	514	260	90	116	11	2	0	0	0	0
13	359	307	150	50	60	6	1	0	0	0
14	845	197	135	47	11	9	1	0	0	0
15	410	472	91	48	12	2	2	0	0	0
16	855	243	266	48	23	5	1	1	0	0
17	649	508	138	141	23	10	2	0	0	0
18	575	377	268	63	55	8	3	1	0	0
19	408	332	196	119	23	17	2	1	0	0
20	418	242	187	102	56	10	7	1	0	0

TABLE 9. Estimates associated with the stock–recruitment relationship for Set 1 with $M = 0.5$.

The estimated coefficients for the Ricker curve

$\alpha = 9.84$ $\delta = 0.0064$

The estimated maximum reproduction is at 0.54 times the estimated average reproductive potential of 290.

The predicted recruitment (for years 5–20)

52	101	151	249	501	567	434	474	567	548
557	552	538	548	552	489				

The estimated residuals for the stock–recruitment

0.02	−0.04	−0.21	0.10	0.70	−0.57	0.05	0.08	−0.46	0.43
−0.31	0.44	0.19	0.05	−0.30	−0.16				

The correlation between the estimated and actual deviations from the stock–recruitment relationship is 0.96.

of the model when it is given the correct aging error probabilities. The second set investigates its performance when it is assumed that there are no aging errors. The third set investigates the effect of grouping the last age classes together. For all three sets the relative reproductive potentials have been assumed known and have been supplied to the model. The first three sets all use the VB parameterization of the fishing mortality. The fourth set is the same as the third except that the Doubleday parameterization of the fishing mortality has been used instead of the VB parameterization.

For all runs, the penalty weights for the stock–recruitment relationship and the deviations from average fishing mortality have been set equal to 2.

The relevant aspects of the simulated fish population are

TABLE 10. The estimated fishing mortality.

The estimated relative fishing vulnerability										
0.047	0.149	0.302	0.470	0.623	0.748	0.844	0.914	0.965	1.000

The estimates of instantaneous fishing mortality

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	0.03	0.09	0.19	0.29	0.38	0.46	0.51	0.56	0.59	0.61
2	0.02	0.06	0.13	0.20	0.27	0.32	0.36	0.39	0.41	0.43
3	0.02	0.06	0.13	0.20	0.27	0.32	0.37	0.40	0.42	0.44
4	0.06	0.19	0.38	0.59	0.78	0.94	1.06	1.15	1.21	1.26
5	0.05	0.17	0.35	0.54	0.71	0.86	0.97	1.05	1.11	1.15
6	0.10	0.31	0.63	0.97	1.29	1.54	1.74	1.89	1.99	2.07
7	0.02	0.06	0.12	0.19	0.25	0.30	0.34	0.37	0.39	0.40
8	0.01	0.05	0.09	0.14	0.19	0.22	0.25	0.27	0.29	0.30
9	0.02	0.07	0.15	0.23	0.30	0.37	0.41	0.45	0.47	0.49
10	0.08	0.24	0.49	0.76	1.01	1.21	1.36	1.48	1.56	1.62
11	0.06	0.19	0.40	0.61	0.81	0.98	1.10	1.20	1.26	1.31
12	0.01	0.05	0.10	0.16	0.20	0.25	0.28	0.30	0.32	0.33
13	0.10	0.32	0.66	1.02	1.36	1.63	1.84	1.99	2.10	2.17
14	0.08	0.27	0.54	0.84	1.11	1.34	1.51	1.63	1.72	1.78
15	0.02	0.07	0.15	0.23	0.31	0.37	0.42	0.46	0.48	0.50
16	0.02	0.07	0.14	0.21	0.28	0.33	0.38	0.41	0.43	0.45
17	0.04	0.14	0.28	0.44	0.58	0.70	0.79	0.86	0.90	0.94
18	0.05	0.16	0.32	0.49	0.65	0.78	0.88	0.95	1.01	1.04
19	0.02	0.08	0.16	0.24	0.32	0.39	0.44	0.47	0.50	0.52
20	0.04	0.12	0.23	0.36	0.48	0.58	0.65	0.71	0.75	0.77

The estimated residuals for the effort-fishing mortality relationship

−0.17	0.17	0.18	−0.37	−0.23	0.13	0.10	−0.19	−0.40	−0.11
−0.10	−0.09	0.18	0.50	0.32	0.21	−0.15	0.37	−0.34	0.06

The correlation between the estimated and actual deviations from the effort-fishing mortality relationship is 0.98.

SET 2: Set 2 is the same as Set 1 except that the model is run under the assumption that there are no aging errors. The results from set 2 are summarized in Tables 11 through 14.

TABLE 11. Value of the objective function for different values of the instantaneous natural mortality M.

M	0.5	0.6	0.7	0.8	0.9	1.0
Objective function	131.6	130.3	129.5	129.4	129.8	130.7

summarized in Tables 1 through 6.

The goodness of fit for the various runs is measured by the log-likelihood function with its sign changed. Thus a smaller value of the objective function denotes a better fit to the observed data.

Summary and Conclusions

We deal first with the results from set 4. Examining the estimated relative fishing vulnerability in Table 19, it is clear that the parameter estimates have become unstable. There is simply not enough information to determine them when the older age classes are grouped together, and a more restrictive parameterization must be used.

We emphasize that we in no way wish to imply that the Doubleday parameterization is of no value. In other situations, the Doubleday, VB, or indeed some other parameterization of the fishing mortality could be the appropriate one.

In evaluating the performance of the model for the other three sets, we shall concentrate on three aspects of the analysis. These are the ability of the model to estimate the instantaneous natural mortality rate M, the ability of the model to synthesize the stock−recruitment relationship, and the ability of the model to detect deviations from average fishing mortality. For comparing the latter two attributes the instantaneous natural mortality rate has been fixed at 0.5 for all three

TABLE 12. The estimated numbers of fish in the population for set 2 with $M = 0.5$.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	773	853	594	295	190	79	19	10	3	0
2	814	456	475	301	134	78	30	7	3	1
3	677	484	261	255	150	62	34	12	3	1
4	349	403	277	140	127	69	27	14	5	1
5	120	200	206	118	48	35	16	6	3	1
6	114	69	105	91	43	14	9	4	1	1
7	172	63	33	37	23	8	2	1	0	0
8	439	103	37	18	19	11	4	1	0	0
9	828	264	61	21	10	10	6	2	0	0
10	468	492	151	32	10	5	4	2	1	0
11	484	265	243	59	10	2	1	1	0	0
12	511	278	136	104	20	3	1	0	0	0
13	506	306	162	76	55	10	1	0	0	0
14	738	282	142	56	18	10	1	0	0	0
15	603	416	136	54	16	4	2	0	0	0
16	810	358	237	72	26	7	2	1	0	0
17	728	482	205	127	36	12	3	1	0	0
18	616	425	259	97	51	13	4	1	0	0
19	483	358	225	119	37	17	4	1	0	0
20	454	287	203	119	58	17	7	1	0	0

TABLE 13. Estimates associated with the stock–recruitment relationship for set 2 with $M = 0.5$.

The estimated coefficients for the Ricker curve

$\alpha = 9.05$ $\delta = 0.0054$

The estimated maximum reproduction is at 0.59 times the estimated average reproductive potential of 311.

The predicted recruitment (for years 5–20)

92	162	227	339	574	610	487	557	616	603
609	608	588	604	602	551				

The estimated residuals for the stock–recruitment

0.27	−0.35	−0.28	0.26	0.37	−0.26	−0.01	−0.09	−0.20	0.20
−0.01	0.29	0.21	0.02	−0.22	−0.19				

The correlation between the estimated and actual deviations from the stock–recruitment relationship is 0.76.

TABLE 14. The estimated fishing mortality.

The estimated relative fishing vulnerability

0.043	0.133	0.281	0.455	0.619	0.754	0.853	0.923	0.969	1.000

The estimated residuals for the effort-fishing mortality relationship

−0.08	0.25	0.25	−0.31	−0.19	0.11	−0.04	−0.42	−0.44	−0.10
−0.09	−0.09	0.16	0.50	0.32	0.22	−0.13	0.38	−0.34	0.04

The correlation between the estimated and actual deviations from the effort-fishing mortality relationship is 0.91

sets in order to make it easier to compare the resulting parameter estimates.

The performance of the model in estimating the instantaneous natural mortality rate is presented in Tables 7, 11, and 15.

Set 1 (Tables 7–10) has the best result with the minimum of the objective function occurring near its true value of 0.5.

Set 2 (Tables 11–14) gives the worst result with the minimum occurring near 0.8. This indicates a strong sensitivity of the estimate of this parameter to the existence of the aging

SET 3: For the runs in set 3 the last seven age classes in the input data were grouped together and the model is run under the assumption that there are no aging errors. The results from set 3 are summarized in Tables 15 through 18.

TABLE 15. Value of the objective function for different values of the instantaneous natural mortality M.

M	0.3	0.4	0.5	0.6	0.7
Objective function	25.1	24.7	24.9	25.5	26.3

TABLE 16. The estimated numbers of fish in the population for set 3 with $M = 0.5$.

	Age									
Year	4	5	6	7	8	9	10	11	12	13
1	423	1039	727	3	585	2	1	11	13	0
2	935	250	579	371	1	264	1	1	5	6
3	680	557	143	310	189	1	127	0	0	2
4	344	405	317	76	156	92	0	60	0	0
5	75	197	204	132	27	50	28	0	17	0
6	90	43	101	88	49	9	16	9	0	5
7	125	50	20	34	23	11	2	3	2	0
8	271	75	29	11	17	11	5	1	1	1
9	1065	162	43	16	6	9	6	3	0	1
10	345	632	91	23	8	3	4	3	1	0
11	487	195	303	35	7	2	1	1	1	0
12	519	279	98	127	12	2	1	0	0	0
13	412	310	162	54	67	6	1	0	0	0
14	986	228	139	53	14	14	1	0	0	0
15	437	557	110	52	16	4	4	0	0	0
16	930	260	317	58	26	8	2	2	0	0
17	755	554	148	171	30	13	4	1	1	0
18	629	441	297	70	72	12	5	1	0	0
19	478	366	233	136	28	27	4	2	0	0
20	453	284	207	123	68	14	13	2	1	0

TABLE 17. Estimates associated with the stock–recruitment relationship for Set 3 with $M = 0.5$.

The estimated coefficients for the Ricker curve

$\alpha = 9.237$ $\delta = 0.5524E\text{-}02$

The estimation maximum reproduction is at 0.55 times the estimated average reproductive potential of 326.

The predicted recruitment (for years 5–20)

56	109	172	291	548	613	465	495	615	605
610	607	594	592	594	530				

The estimated residuals for the stock–recruitment are

0.29	−0.18	−0.32	0.07	0.66	−0.57	0.05	0.05	−0.40	0.49
−0.33	0.43	0.24	0.06	−0.22	−0.16				

The correlation between the estimated and actual deviations from the stock–recruitment relationship is 0.98.

errors if they are not accounted for.

Set 3 (Tables 15–18) gives a good result with an estimate of M near 0.4.

The fact that the objective function decreased from 129.4 to 84.2 when the correct aging error probabilities were incorporated into the model indicates that at least in some cases it might be possible to use the model to estimate the aging error probabilities. On the other hand the fact that M was estimated better in set 3 than in set 2 indicates that if the aging error probabilities are unknown or cannot be estimated for the older fish, then it is better to use only the age structures for the younger fish which are aged almost without error and to group the older fish together.

The performance of the model in synthesizing the stock–

TABLE 18. The estimated fishing mortality.

The estimated relative fishing vulnerability									
0.074	0.245	0.496	0.714	0.853	0.929	0.968	0.987	0.996	1.000
The estimated residuals for the effort-fishing mortality relationship									
−0.179	0.184	0.232	−0.314	−0.200	0.154	0.142	−0.121	−0.335	−0.079
−0.098	−0.070	0.178	0.430	0.241	0.151	−0.197	0.302	−0.404	0.002

The correlation between the estimated and actual deviations from the effort-fishing mortality relationship is 0.98.

SET 4: Set 4 is identical to set 3 except that the Doubleday parameterization of the fishing mortality has been used instead of the VB parameterization. The results for set 4 are given in Table 19.

TABLE 19. The estimated relative fishing vulnerability.

0.084	0.251	0.519	0.734	1.000	0.389	0.884	0.844	0.069	0.002

recruitment relationship is presented in Tables 9, 13, and 17. The correct parameters of the stock−recruitment relationship are presented in Table 6.

In all three sets the model was able to identify with good accuracy the relationship between the maximum reproduction and the estimated average reproductive potential. This is important because it is this information which indicates whether heavier exploitation will result in an increase or decrease in the expected recruitment.

Another point to be considered when examining the stock−recruitment relationship is the ability of the model to estimate correctly the residuals. They are important because if environmental factors affecting the recruitment process are to be detected, it is necessary for the model to estimate the residuals well.

In set 1 the correlation between the actual and estimated residuals was 0.96. In sets 2 and 3 it was 0.76 and 0.98, respectively. Thus the effect of not accounting for the aging errors was to reduce to a considerable degree the ability of the model to estimate these residuals, and it is again demonstrated that for some quantities the estimates are better if the older ages are grouped if the aging errors are not to be taken into account.

The effect of the aging errors can be seen clearly by comparing Tables 1 and 12 for the estimated number of 4-yr-old fish in the population, where it can be seen that they produce a characteristic smoothing of these estimates.

The deviations from average fishing mortality are important because they must be well estimated to detect such phenomena as variations in fleet efficiency or catchability.

The actual deviations from average fishing mortality are given in Table 5. The estimated deviations from average fishing mortality are given in Tables 10, 14, and 18. For the three sets the respective correlations were 0.98, 0.91, and 0.98. Thus once again grouping the ages together gives better results than ignoring the aging errors.

One point has been made. The process of aging fish to obtain information about the age structure of the catch is expensive and time consuming. This data should not be produced without considering the final use to which it will be put. If this final use is an age-structured model, then aging a large number of older fish "almost" accurately, although a triumph of laboratory procedure, may not only be a waste of money and effort, but may actually degrade the quality of the estimates obtained from the age-structured model.

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Appendix. Symbols Used

i	=	Indexes years
n	=	The number of years
j	=	Indexes the age classes
r	=	The number of age classes
C_i	=	The actual number of fish caught in year i
C_{ij}	=	The actual catch of age class j fish in year i
N_{ij}	=	The actual number of fish from age class j in the population at the beginning of year i
F_{ij}	=	Instantaneous fishing mortality
M_{ij}	=	Instantaneous natural mortality
P_{ij}	=	The percentage of the fish caught in year i which belong to age class j
O_i	=	The estimated total number of fish caught in year i
S_{ij}	=	The number of fish aged in year i and found to be of age j
D_i	=	The deviation from average fishing mortality in year i
σ	=	The standard deviation for errors in total catch estimates
σ_1	=	The standard deviation for deviation from average fishing mortality
σ_2	=	The standard deviation for the stock−recruitment relationship

A Statistical Method for Evaluating the Reproducibility of Age Determination

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CHANG, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39: 1208–1210.

The coefficients of variation and the index of precision provide a statistical test of reproducibility of aging between readers. Because the coefficients of variation and the index of precision incorporate the averaged year-class of a fish species, they are free from the shortcoming of the percent agreement method. Because variance is a better estimator than absolute difference, the coefficient of variation is a stronger estimator than the index of average percent error in providing a test statistic.

Key words: age determination, coefficients of variation, index of precision, average percent error, percent agreement

CHANG, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39: 1208–1210.

Les coefficients de variation et l'indice de précision permettent de vérifier statistiquement la reproductibilité des déterminations d'âge par des chercheurs différents. Comme ces deux paramètres incorporent la moyenne des classes d'âge d'une espèce de poissons, ils sont exempts des imperfections que l'on rencontre dans la méthode du pourcentage de lectures identiques. La variance étant un meilleur estimateur que la différence absolue, le coefficient de variation est supérieur à l'indice d'erreurs moyennes de pourcentage comme méthode de vérification statistique.

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METHODS to test the reproducibility of the results from scale reading to determine fish age are many. One of the common techniques to assess the precision of fish age estimated from scale readings is to compare the percentages of determination of age which are agreed upon by several readers (Kennedy 1970). However, this technique has a disadvantage because it fails to take into consideration the range of fish year-class as available to the fishery. Beamish and Fournier (1981) pointed out this problem and showed that if 95% of age determinations between two readers agree within ±1 yr for Pacific cod (*Gadus macrocephalus*), this can be very poor precision as most commercial samples are made up of fish within a narrow age range. On the other hand, if 95% of spiny dogfish (*Squalus acanthias*) age determinations agree within ±5 yr, this can represent good precision as dogfish may be as old as 60 yr with ~30 age-groups in a fishery. Nonetheless, this example involves a tacit assumption that the range of fish year-class available to the fishery increases in proportion to the average age of fish in the fishery, or, in other words, that the standard deviation is proportional to the mean. Beamish and Fournier (1981) proposed a method based on this assumption and incorporating the range of year-class into the computation of their index, which uses the average absolute deviation from the arithmetic mean age per fish expressed as a function of the arithmetic mean. This paper more explicitly suggests an alternative index which provides a statistical test of reproducibility of aging between readers.

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Methods — An average percent error (APE) in aging the jth fish is shown in Beamish and Fournier (1981) as

$$(1)\quad \frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}$$

where X_{ij} is the ith age determination of the jth fish, X_j is the average age calculated for the jth fish, and R is the number of times each is aged.

This paper suggests the use of a coefficient of variation (V) for testing the reproducibility of aging between readers. The coefficient of variation is the standard deviation as a fraction of the mean expressed as a percentage and may be obtained by replacing the average absolute deviation from the arithmetic mean age in equation (1) with the standard deviation. Because V is greater than APE by $\left(\frac{(\Sigma X_{ij}-X_j)^2}{R(R-1)}\right)^{1/2}\Big/X_j$, the estimates from V are always greater than those from APE by the same quantity. The percent error contributed by each observation to the average age-class may be estimated by an index of precision (D), which is V divided by $\sqrt{R}$ (Elliott 1977; Sokal and Rohlf 1969).

Standard methods for testing the variability of two readers in this situation include the use of the coefficient of variation, or the log transformation approach to the standard error of the mean (Zar 1974; Sokal and Rohlf 1969).

Results and Discussion — The advantages of the index of average percent error (APE) in determining the reproducibil-

TABLE 1. Example of a set of walleye pollock (*Theragra chalcogramma*) ages using the fin-ray method (Beamish and Fournier 1981).[a]

Fish No.	Reader 1						Reader 2					
	1st	2nd	3rd	APE	*V*	*D*	1st	2nd	3rd	APE	*V*	*D*
1	7	6	7	0.0667	0.0866	0.0501	6	5	6	0.0784	0.1019	0.0589
2	7	6	6	0.0717	0.0912	0.0527	6	5	6	0.0784	0.1019	0.0589
3	6	6	5	0.0784	0.1019	0.0589	5	4	6	0.1333	0.2000	0.1156
4	4	4	4	0.0	0.0	0.0	4	4	3	0.1212	0.1575	0.0910
5	4	5	6	0.1333	0.20	0.1156	6	5	5	0.0833	0.1083	0.0626
6	3	3	3	0.0	0.0	0.0	3	3	2	0.1667	0.2165	0.1251
7	5	5	5	0.0	0.0	0.0	5	4	5	0.0952	0.1237	0.0715
8	4	4	4	0.0	0.0	0.0	5	4	4	0.1026	0.1332	0.0770
9	4	4	4	0.0	0.0	0.0	4	3	3	0.1333	0.1732	0.1001
10	7	8	7	0.0606	0.0787	0.0455	6	5	7	0.1111	0.1667	0.0963
11	7	7	7	0.0	0.0	0.0	7	5	6	0.1111	0.1667	0.0963
12	3	2	3	0.1667	0.2165	0.1251	3	2	3	0.1667	0.2165	0.1251
13	5	5	5	0.0	0.0	0.0	5	4	4	0.1026	0.1332	0.0770
14	4	4	4	0.0	0.0	0.0	5	2	4	0.3030	0.4166	0.2408
15	6	6	4	0.1667	0.2165	0.1251	6	4	5	0.1333	0.2000	0.1156
16	7	7	7	0.0	0.0	0.0	5	6	5	0.0833	0.1083	0.0626
17	6	6	5	0.0784	0.1019	0.0589	5	5	5	0.0	0.0	0.0
18	7	7	7	0.0	0.0	0.0	7	6	6	0.0702	0.0912	0.0527
19	8	7	7	0.0606	0.0787	0.0455	7	5	5	0.1569	0.2038	0.1178
20	5	5	5	0.0	0.0	0.0	5	4	5	0.0952	0.1237	0.0715
$\bar{x}$				0.0441	0.0586	0.0339				0.1163	0.1571	0.0983

[a]Where APE is the average percent error using the index of Beamish and Fournier: *V* is the coefficient of variation; and *D* is an index of precision.

TABLE 2. The frequencies with which the age assigned by the first reader differed from that assigned by the second reader using the set of data presented in Table 1.

Age difference	No.
−3	0
−2	1
−1	4
0	23
+1	23
+2	8
+3	1
Percent agreement in the age assigned within ±1 yr	83.3
Percent agreement in the age assigned within ±2 yr	98.3

ity of age determination is shared by the coefficients of variation (*V*) and the index of precision (*D*). These indices agree closely, particularly between APE and *D* (Table 1). Reader 1 has a greater precision in APE than Reader 2; the same relationship is shown in the averaged values of the coefficients of variation and in the index of precision between these readers. Because the coefficients of variation and the index of precision are indices which incorporate the averaged year-class of fish, they are free from the disadvantage of a percent agreement technique. In Table 2, for example, one can see that using the same set of data presented in Table 1, the percent agreement technique shows considerable precision between two readers in the age determination; 83% agreed within 1 yr and 98% within 2 yr. However, if one uses the coefficient of variation, an index of precision, and the index of average percent error (Table 1), the difference between two readers is remarkable.

There are additional benefits in using the coefficients of variation and the index of precision in the examination of reproducibility of age determination. First, variance is a better estimator than absolute difference as it is an unbiased and consistent estimator, the mean and variance of which converge as sample size increases; the coefficient of variation for all practical purposes shares this property (Simpson et al. 1960). Second, the index of precision (D_j) can be used to show the percent error contributed by each observation to the averaged age determination for the *j*th fish; if one multiplies the index of precision (D_j) by the averaged age for the *j*th fish, the result is the error in age determination made for each observation.

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Nutrient Distributions and Their Relationships to Water Masses in Baffin Bay

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COOTE, A. R., AND E. P. JONES. 1982. Nutrient distributions and their relationships to water masses in Baffin Bay. Can. J. Fish. Aquat. Sci. 39: 1210–1214.

We report measurements of phosphate, nitrate, and silicate concentrations in Baffin Bay and relate them to water masses identified by salinity and temperature. Our results illustrate the remarkable homogeneity of the water structure throughout Baffin Bay and show that nutrient concentrations can be used to label water masses in the Baffin Bay deep layer with similar resolution to that provided by salinity and temperature.

Key words: phosphates, nitrates, silicates, Baffin Bay, water masses, nutrient concentrations

COOTE, A. R., AND E. P. JONES. 1982. Nutrient distributions and their relationships to water masses in Baffin Bay. Can. J. Fish. Aquat. Sci. 39: 1210–1214.

On présente ici le résultat de dosages de phosphates, nitrates et silicates dans la baie Baffin et on établit la relation entre ces derniers et les masses d'eau telles qu'identifiées par la salinité et la température. Nos resultats démontrent bien la remarquable homogénéité de la structure de l'eau dans toute la baie. Ils indiquent également que les concentrations de nutriments peuvent servir à identifier les masses d'eau de la couche profonde avec une résolution semblable à celle que fournissent la salinité et la température.

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PHOSPHATE, nitrate, and silicate concentrations have been measured throughout Baffin Bay. Previously reported results from the Canadian Archipelago showed that these nutrients were able to distinguish between water masses flowing into Baffin Bay that would not otherwise have been easy to identify from salinity and temperature measurements alone (Jones and Coote 1980; Codispoti 1979; Codispoti and Owens 1975). Our aim in this paper is to describe the distribution of nutrients in Baffin Bay and to relate nutrient concentrations to the water masses found there.

Some previous nutrient measurements have been reported for Baffin Bay. These were made at several stations in the Northwater region, south of Smith Sound, and at a few stations in the south central region (McGill and Corwin 1964; Corwin and McGill 1963). These earlier measurements, however, are not complete enough or, for phosphate and nitrate concentrations, precise enough for a reasonable characterization of the water in Baffin Bay.

Methods — Samples for nutrient measurements were collected during the summer season (August and September, 1977) at several locations in Baffin Bay (Fig. 1). They were analyzed within a few hours of collection using standard methods (Strickland and Parsons 1968) with an AutoAnalyzer II. Sampling error was monitored by analyzing duplicate samples for about 1-in-10 samples. Analytical precision was ±0.4 μg-at./L for nitrate and silicate concentrations and ±0.02 μg-at./L for phosphate concentrations. Accuracy was monitored with CSK standards and is believed to be within twice this range. Salinity and temperature values were measured using a Guildline Mk. III analogue CTD system (salinity precision ≈0.01‰, temperature precision ≈0.01°C). Temperatures were also measured at selected depths using both protected and unprotected reversing thermometers. Salinity values were determined for all samples using a Guildline Autosal model 8400 salinometer (salinity precision ≈0.002‰).

Results and discussion — Our results are illustrated by three section plots: northern Baffin Bay, central Baffin Bay, and Davis Strait (Fig. 2). Near-surface features, above about 25 m, are omitted in these figures. Where they can be compared, our silicate concentrations are within about 2% of the earlier results (Corwin and McGill 1963; McGill and Corwin 1964). Our nitrate concentrations tend to be slightly lower and both our nitrate and phosphate concentrations show less scatter when plotted against salinity. The reduced scatter is probably due to using more modern analytical techniques and to analyzing the samples soon after collection instead of preserving them for much later analysis in the laboratory.

To consider the relationship of nutrient concentrations to the water masses in Baffin Bay, we first summarize the physical oceanography of Baffin Bay (Coachman and Aagaard 1974; Muench 1971). Water flows into Baffin Bay from the Arctic Ocean through Lancaster and Jones Sounds over sills of about 150 m and through Nares Strait (at Smith Sound)

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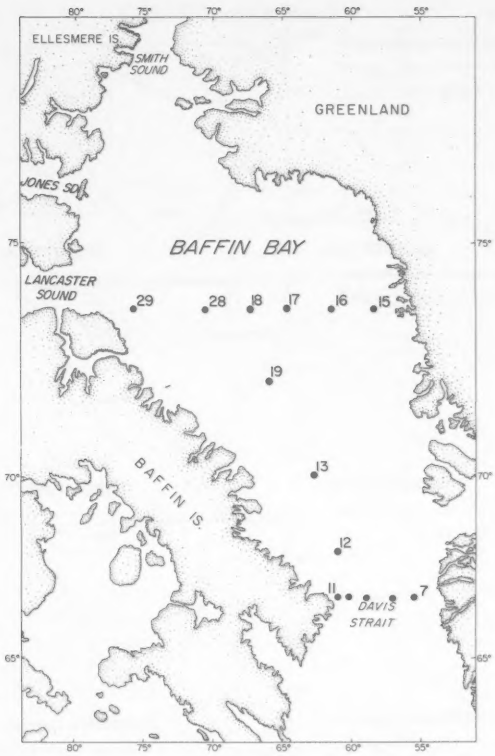

FIG. 1. Schematic map showing locations of oceanographic stations. Stn. 7: 66°45.1′N, 55°25.1′W; Stn. 8: 66°45.4′N, 57°05.7′W; Stn. 9: 66°44.2′N, 58°58.2′W; Stn. 10: 66°44.9′N, 60°15.9′W; Stn. 11: 66°45.3′N, 61°02.9′W; Stn. 12: 68°08.7′N, 61°21.3′W; Stn. 13: 70°02.3′N, 62°46.1′W; Stn. 15: 73°41.8′N, 58°39.5′W; Stn. 16: 73°41.2′N, 61°38.6′W; Stn. 17: 73°42.0′N, 64°34.9′W; Stn. 18: 73°40.2′N, 67°17.3′W; Stn. 19: 72°14.1′N, 65°56.9′W; Stn. 28: 73°42.0′N, 70°29.0′W; Stn. 29: 73°42.0′N, 75°55.0′W.

over a sill of about 250 m. Water also enters Baffin Bay from the Atlantic Ocean by way of the West Greenland Current in eastern Davis Strait. Water leaves Baffin Bay by way of the Baffinland (or Canadian) Current in western Davis Strait. The near-surface circulation within Baffin Bay is northward in the eastern part (West Greenland Current) and southward in the western part (Baffinland Current) with some more complicated flow especially in the northern region. Northern Baffin Bay is characterized by the Northwater region, a large polynya extending roughly from Smith Sound to the entrance to Jones Sound. The central region of Baffin Bay tends to have ice cover most of the year.

Muench (1971) described the water in Baffin Bay in terms of upper, intermediate, and deep layers. The deep layer includes Baffin Bay Bottom Water, water below about 1800 m, which has almost constant salinity (34.50‰) and temperature (−0.33°C). Water in the upper layer is formed from both Arctic Ocean water which has entered through the Canadian Archipelago and Atlantic water which has entered through Davis Strait and has been diluted by runoff and cooled. Water in the intermediate layer is Atlantic water which has also entered through Davis Strait, but has lost heat and undergone some mixing with the Arctic Ocean water. The deep layer is thought to be Arctic Ocean water of Atlantic origin which has pulsed through Smith Sound at irregular intervals (Muench 1971). The origin of the bottom water, below 1800 m, is not known for certain, though it could quite likely also be Arctic Ocean water of Atlantic origin which has entered Baffin Bay at irregular and infrequent intervals (Sadler 1976; Muench 1971).

Many of the characteristics of the water in Baffin Bay as described by Muench (1971) are shown in Fig. 2. The three layers are discernible in the salinity and temperature sections. In addition, we can see a cold core of water between about 50 m and 200 m capped by a very shallow layer of warmer, fresher water. The cold core likely results from cooling during the previous winter, while the warmer, fresher water is produced by summer heating and the introduction of sea ice meltwater into the water column. In Davis Strait, one can recognize three types of water. In the west above about 300 m is the cold water of the Baffinland Current flowing out of Baffin Bay. In the east is the warmer, more saline Atlantic water of the West Greenland Current flowing into Baffin Bay. Underlying both of these, below about 300 m in the west and 600 m in the east, is water very similar to that in central Baffin Bay at the same depths.

The nutrient concentrations (Fig. 2) reflect the same structure as do salinity and temperature, although the three layers are not perhaps quite so distinctly illustrated. In the northern and central sections both nitrate and phosphate concentrations increase about 50% with depth from below the upper layer to the bottom whereas silicate concentrations increase nearly fourfold between these depths. The relationship between water masses as characterized by temperature−salinity plots and nutrient−salinity plots is shown in Fig. 3. The division between the layers described by Muench (1971) on the T−S diagrams are transcribed to the nutrient−salinity plots to maintain the same identification of sample with water type. In Davis Strait, there is additional water from the Atlantic. What is very clear is that the water masses characterized by temperature and salinity can also be well characterized by nutrients and salinity. For example, with an optimum precision of 0.005°C in temperature, which is probably the best that could be achieved at present, and 0.4 μg-at./L in silicate concentrations, the spread of values in T−S diagrams which defines the deep layer corresponds to a similar spread of values in the silicate−salinity plots. Almost as good resolution is obtained also for phosphate and nitrate measurements. Thus with nutrients one has the opportunity to classify water types equally well with nutrients as with temperature. In contrast to results from the Canadian Archipelago (Jones and Coote 1980), however, nutrient concentrations in Baffin Bay do not give particularly new insight into water mass sources or circulation patterns.

Another revealing feature of these plots is the remarkable uniformity of the water at different locations throughout Baffin Bay. There is little variation between stations across

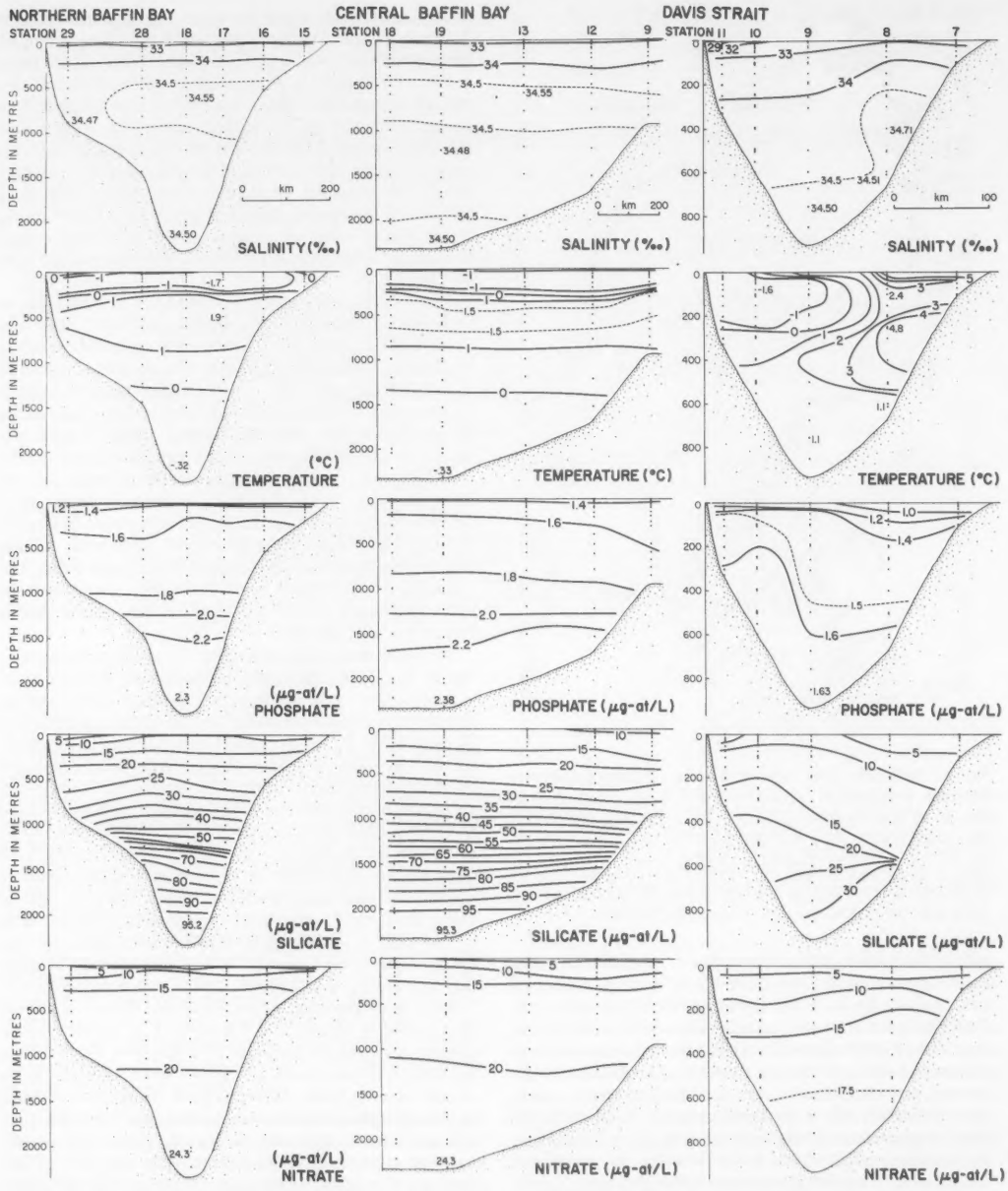

FIG. 2. Sections for Northern Baffin Bay, Central Baffin Bay, and Davis Strait: salinity, temperature, phosphate, silicate, and nitrate.

northern Baffin Bay and little to distinguish Station 18 in the northern section from Station 12 near the south. Even near the sill in Davis Strait, the water at Station 9 is not much different from the water at Station 18 at similar depths. Thus the water in one part of Baffin Bay is very similar to water in another part, at least below the immediate surface region. Also, as is

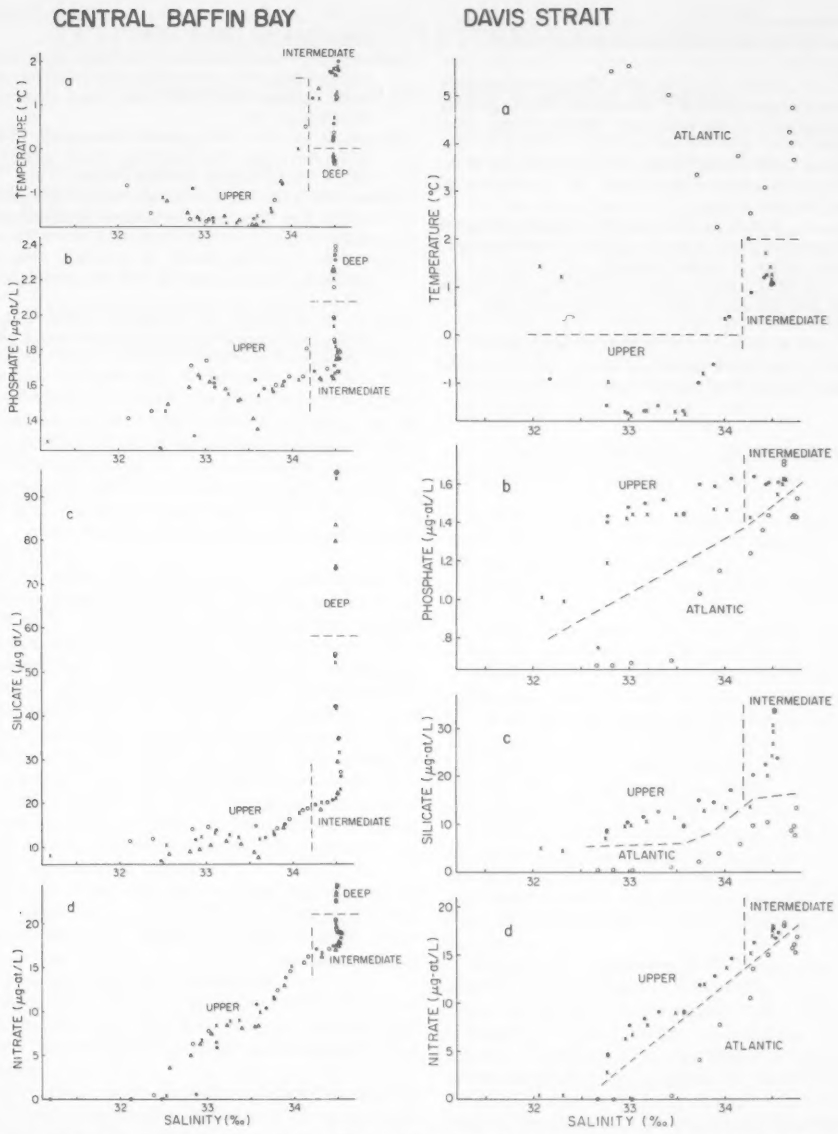

FIG. 3. Central Baffin Bay (Stations 12(△), 13(x), 18(●), and 19(○). Davis Strait (Stations 8(○), 9(x), and 10(●). (a) Temperature vs. salinity, (b) phosphate vs. salinity, (c) silicate vs. salinity, (d) nitrate vs. salinity.

shown by helium–tritium measurements (Top et al. 1980), the water has increasingly long residence times at greater depths, reaching a maximum of a few hundred years for Baffin Bay bottom water (Top et al. 1980). These two features tend to reduce the number of considerations which usually enter into discussions of chemical processes and suggest that Baffin Bay may be a good "laboratory" for studying chemical processes in the ocean. As well, if water masses can be more precisely dated, Baffin Bay may provide opportunities to study changes in atmospheric input of chemicals into the ocean that have occurred over the last few decades or centuries (e.g. Jones and Levy 1981).

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LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on Reeve M. Bailey's View of Lamprey Systematics

COMMENT

BAILEY (1980) commented on our views, and those of Dr I. C. Potter, concerning the classification and nomenclature of lampreys. In the following discussion we have selected the principal statements presented by Bailey with which we cannot agree.

Lampetra zanandreai Vladykov

In 1955 the senior author described a new species of brook lampreys from northern Italy. It represents a third European species of the genus *Lampetra*. The absence of a row of small teeth (posterials) on the posterior field of the disk, and the frequent occurrence of the tricuspid middle endolateral tooth, the typical formula being 2−3−2, prevented the placement of this lamprey in the genus *Lethenteron*, species of which have a row of posterials and the endolateral formula 2−2−2. We follow the teeth nomenclature as published by Vladykov and Follett (1967).

Zanandrea (1958) published a paper with surprising and incredible statements for us, that in several metamorphosed specimens of *L. zanandreai*, he observed the presence of a complete or partial row of posterials. However, on two of his photographs of the *L. zanandreai* disk (Plate I), no posterials are detectable. On his schematic drawings, he indicated the endolateral formula as 2−2−2. In short, *L. zanandreai* can be considered as belonging to the genus *Lethenteron*. This suggestion is contrary to the original description of the species by Vladykov (1955). On the other hand, Hubbs and Potter (1971: 53) made the statement: "*L. zanandreai* is an isolated relict form of the *Lethenteron* series." Bailey (1980) also agreed with them. To bring to light the truth about *L. zanandreai*, we must make the following statements.

1) Hubbs and Potter[1] and Bailey gained their information on *L. zanandreai* only from Zanandrea's (1958) paper. They never approached us to borrow specimens of north Italian lampreys for detailed study. In other words, the above authors lack personal knowledge of *L. zanandreai*.

2) In the bibliography given by Bailey (1980), the papers by Zanandrea (1961) and Vladykov (1973) are not mentioned. Both papers have direct bearings on the taxonomic position of *L. zanandreai*.

Zanandrea (1961), on the basis of very extensive material, about 1500 metamorphosed individuals of *L. zanandreai*, reached the conclusion that: "all brook lampreys caught in the waters of north Italian plain have the characters on which Vladykov founded the species *L. zanandreai*, i.e. number and disposition of teeth on oral disc, number of trunk myomeres. . .".

By the above remarks Zanandrea retracted his previous incorrect statement that *L. zanandreai* has posterials (Zanandrea 1958). It must be added that in 1962 in Rome, Vladykov discussed with the late G. Zanandrea the presence of posterials in *L. zanandreai*. Dr Zanandrea then said "on examining freshly caught *L. zanandreai* I saw posterials, but when the specimens were put in formalin these teeth disappeared." This is very surprising as horny lamprey's teeth do not dissolve either in formalin or alcohol. For further details see Vladykov (1973) and Potter (1980).

Newly described species of Lethenteron and Entosphenus genera by Vladykov and collaborators

In 1975, Vladykov et al. described a new species, *Lethenteron meridionale*, from freshwater streams of the Gulf of Mexico. During 1978, two more species of the same genus were described by Vladykov and Kott, *L. matsubarai* (1978b) and *L. alaskense* (1978a).

Among new species of *Entosphenus* published by Vladykov and Kott, the following should be mentioned: *E. folletti* (1976b), *E. hubbsi* (1976d), and *E. similis* (1979a).

The description of each of these new species was based by us on detailed studies of different morphological and anatomical characters, particularly details of their dentition and peculiarities of velar tentacles (Vladykov and Kott 1976c). Their geographical distributions and relationships with closely related forms were also included.

Bailey (p. 1629), without giving a valid reason for his inclusion of our *Entosphenus* species in the genus *Lampetra* and with disregard to our detailed descriptions, summarily considered them as only "nominal species." On the other hand, Potter (1980: 1603−1606) accepted the validity of all our species.

Phylogenetic relationship of Petromyzontidae is complicated by the fact that six polyspecific genera represent a mixture of parasitic and nonparasitic forms. For the latter, we (Vladykov and Kott 1979b) proposed the term "satellite species." Thus satellite species represent nonparasitic forms which morphologically resemble the parasitic (stem) species from which they are probably derived. Some of them exhibit varying degrees of morphological differentiation from the stem species. There is no evidence that one satellite species evolved into another. Rather, each developed independently from the same parasitic species (Vladykov and Kott 1979b; Potter 1980). However, the differentiation of individual satellite species took place at different points in time and in different areas. From the above remarks it appears that the usual type of phylogenetic tree, illustrating the relationship between parasitic and satellite species among lampreys, is not applicable. For this reason we used "circles and connecting lines." For further details see Vladykov and Kott (1979b).

[1]Dr I. C. Potter has since informed the editors that he has seen specimens of *L. zanandreai* which were presented by Dr Zanandrea to Dr M. W. Hardisty; however, their condition and the extreme degeneracy of their dentition prevented Potter from resolving the question of the posterior circumorals.

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Hardisty and Potter (1971) and Potter (1980) suggest that nonparasitic species (satellite species) have a more variable dentition than the stem species, because there is a reduction in the selection pressure which tends to stabilize the functional arrangement of teeth in parasitic species. Bailey (1980), in proposing his classification of lampreys, does not comment on the distinctiveness of the dentition of the various parasitic forms, but emphasizes the dentition of highly degenerative satellite species.

Status of Okkelbergia Creaser and Hubbs, 1922

After critical study, Vladykov and Kott (1976a) reached the conclusion that there are no morphological or anatomical differences between *Okkelbergia* Creaser and Hubbs and *Lampetra* Gray. Therefore *Okkelbergia* is considered by them to be a junior subjective synonym of *Lampetra* and not a distinct genus. Potter (1980) agreed with us and does not now consider *Okkelbergia* as a distinct taxon, either as a genus or a subgenus. Bailey (p. 1629), however, considered that "*Okkelbergia* may for the present be recognized as a subgenus of *Lampetra*, probably the most degenerate (or specialized) of lampreys."

Splitting versus lumping

Among Petromyzontidae, we (Vladykov and Follett 1967; Vladykov and Kott 1979c) recognized eight separate and clearly defined genera, whereas Bailey (p. 1627) favored only four. He wrote (p. 1629) "the arrangement of Vladykov and Kott is a splitter's classification; they do not use the rank of subgenus and upgrade other groups unnecessarily." In contrast, we could name Bailey's arrangement of lamprey families as a "lumper's classification."

In the case of Petromyzontidae, Bailey (p. 1627–1629) favors an unusually broad genus *Lampetra* (sensu lato) in which he includes six subgenera: *Lampetra*, *Okkelbergia*, *Lethenteron*, *Entosphenus*, *Tetrapleurodon*, and *Eudontomyzon*. However, he made the following assessment of his own taxonomic arrangement: "interrelationships among the six suggested subgenera of *Lampetra* are not well understood." Then, what is the advantage of proposing this arrangement?

A principle disadvantage of a lumper's classification is the fact that inclusion of several groups with heterogeneous characters in the same genus hides individual peculiarities of each of the smaller groups.

An example is the absence of posterials in *Lampetra* (s.s.) and their presence in one or several rows in the remaining genera of Petromyzontidae, and the variation in the number of endolateral teeth, etc. There is also a great disadvantage from a distributional point of view. Using Bailey's unusually large genus *Lampetra*, it appears that the representatives of it are found on three continents: North America, Asia, and Europe. This is an erroneous fact, as species of *Lampetra* (s.s.) are absent from Asia.

What are the correct scientific names for the American brook lamprey and the least brook lamprey?

Hubbs and Trautman (1937: 24) recommended *Lampetra lamottenii* (Lesueur) as the correct scientific name for the American brook lamprey, formerly called *Entosphenus appendix* (DeKay). Their recommendation was accepted by most lamprey students. However, Bailey (p. 1629) considered *Lampetra lamottenii* (Lesueur) "as unidentifiable," and recommended its suppression. He also recommended the adoption of the name *Lampetra appendix* (DeKay). His reason is rather surprising, as Lesueur's (1827) description is longer, and contains more details, than that by DeKay (1842). The recommendation by Bailey apparently was made without consideration of the taxonomic importance of the urogenital papilla in males.

The American brook lamprey differs from the least brook lamprey by the following characters: a higher number of trunk myomeres (65–74) and a strong dentition with the endolateral formula 2–2–2. Its spawning males possess, in contrast to those of the least brook lamprey, a very short urogenital papilla, the length of which is 9.4 (4.5–16.7)% of the branchial length.

Because the descriptions by Lesueur (1827), DeKay (1842), and Abbott (1860) do not fit the American brook lamprey, we recommend the adoption of *Lethenteron wilderi* (Gage, 1896) as its correct scientific name. For further details see Vladykov and Kott (1982).

The least brook lamprey in addition to its small size, low trunk myomere count (50–59), and weak dentition has a typical endolateral formula of 2–3–2. Its most important character is the presence in spawning males of a very long urogenital papilla, the length of which is 38.8 (25.0–57.7)% of the branchial length.

By careful study of the texts of Lesueur, DeKay, and Abbott, we reached (Vladykov and Kott 1982) the conclusion that these early authors described under different names the same species which is presently known as "least brook lamprey." According to the rule of priority, it should be called *Lampetra lamottenii* (Lesueur, 1827). However, Hubbs and Trautman (1937: 24) used *Lampetra aepyptera* (Abbott), and subsequent authors followed their recommendation. To avoid possible confusion in nomenclature, we subscribe to the specific name of *aepyptera* (Abbott). This decision is justified by the fact that the type of *aepyptera* was redescribed by Fowler (1901: 328; 1908: 466), who gave the number of trunk myomeres characteristic of the species.

In conclusion, we must repeat that no author, not even one of Dr Reeve M. Bailey's caliber, is protected from erroneous conclusions, if he has not studied the specimens himself, but has only relied on published data — VADIM D. VLADYKOV, *Department of Biology, University of Ottawa, Ottawa, Ont. K1N 6N5* AND EDWARD KOTT, *Wilfrid Laurier University, Waterloo, Ont. N2L 3C5*.

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REPLY

Drs Vladykov and Kott have addressed their discussion to points of disagreement with my comments (Bailey 1980). It may be noted, however, that that communication touched on some points on which we differed in the SLIS symposium volume but that have since been resolved. Notably, the International Commission on Zoological Nomenclature has ruled that the appropriate stem for the family group name is Petromyzont-, hence Petromyzontidae (R. V. Melville, British Museum (Nat. Hist.) London, England, personal communication), a usage now adopted by Vladykov and Kott. My position on most points was, I believe, adequately stated in the 1980 "comments." Nevertheless, I respond to their strictures in an attempt to clarify possible misunderstanding.

Lampetra zanandreai Vladykov

The systematic placement of the distinctive brook lamprey of the Pò River basin, northern Italy, is in dispute. Vladykov (1955, 1973) and Vladykov and Kott (1982) assign it to *Lampetra* (s.s.), whereas Hubbs and Potter (1971: 53), Potter (1980), and Bailey (1980) place it in *Lampetra*, subgenus *Lethenteron*. The decision rests on (1) character differences between these two generic or subgeneric taxa, and (2) divergent views on these characters in *zanandreai*.

Lampetra and *Lethenteron* were distinguished by Vladykov and Follett (1967: 1074) by two characters: the absence in *Lampetra* of posterials (also called posterior circumorals or mandibular labials), present in *Lethenteron*; and the anterior and posterior inner laterals (lateral circumorals) typically bicuspid, the middle tricuspid in *Lampetra* whereas all three inner laterals are bicuspid in *Lethenteron*. The second character, being variable, may be dismissed as useless at the generic or subgeneric level though valuable for distinguishing some species. Vladykov and Follett (1965: 145) had already shown that in their new species *Lampetra richardsoni*, the middle lateral circumoral is typically bicuspid (in 91% on one or both sides of the disk among 23 specimens); they cited Zanandrea (1958: 211), who found among 47 specimens of *L. planeri*, 40 (85%) with the middle lateral circumoral tricuspid on one or both sides. Thus, in one species (*richardsoni*) of *Lampetra* (s.s.) the middle lateral circumoral is usually bicuspid; in *L. fluviatilis*, *L. planeri*, and *L. ayresi*, this tooth is typically tricuspid, but the Pacific brook lamprey *L. pacifica* Vladykov (1973: 208) was reported to have 2 or 3 cusps on the right side, usually 1 or 2 on the left. *Lampetra zanandreai* was said by Vladykov (1955) to have the middle of the 3 enlarged lateral teeth typically tricuspid. However, in 232 specimens Zanandrea (1958: 211) counted 2 cusps on both sides in 192, 2 cusps on one side and 3 on the other in 14, and 3 cusps on both sides in 26; thus, 206 (89%) had 2 on at least one side. In this character *zanandreai* fits Vladykov and Follett's key to *Lethenteron*.

In the remaining character, a reductional feature, five

species of *Lampetra* (s.s.) appear always to lack teeth in the posterior part of the circumoral row: *L. fluviatilis* and *L. planeri* from *Europe* and *L. ayresi*, *L. richardsoni*, and *L. pacifica* from western north America. The species assigned to *Entosphenus*, *Tetrapleurodon*, *Eudontomyzon*, and *Lethenteron* typically have this row well developed. Variations probably depend on whether or not the teeth have erupted from the mucosa of the disk. Vladykov and Kott (1979) assigned to *Lampetra* (s.s.) two species in which they contend posterior circumoral teeth are never present: *L. aepyptera* (see below) and *L. zanandreai*. Presumably because Vladykov (1955) failed to see posterior circumorals in his sample of 19 transformed specimens of *zanandreai*, he and Kott dispute the detailed data presented by Zanandrea (1958), who reported that 74 (41%) of 180 specimens examined have small teeth in the region of the lower lip, "between the infraoral lamina and the ring of circumlabial [marginal] teeth. . . . .these small teeth have the same dimensions as those of the circumlabial ring (fig. 1)." [my translation from the original Italian]. The disposition of these teeth was shown in two specimens by Zanandrea (1958, fig. 1−2). It is not surprising that Vladykov (1955) failed to note these teeth in his sample. Nevertheless, Zanandrea did see them in some animals already preserved and sent to him from Pavia. Vladykov and Kott chide me (and also Hubbs and Potter) for lack of personal knowledge of *L. zanandreai* and for overlooking pertinent papers. Their attack, however, is basically a denial of the reliability of Zanandrea's data. Zanandrea employed a technique (staining narcotized specimens with methylurethane) that revealed posterior circumoral teeth in some specimens; Vladykov and Kott did not. Nor did they indicate attempts to stain or section preserved specimens in search of teeth that might be deeply imbedded in the disk mucosa. Their failure to observe these teeth was interpreted as proof of absence. However, in the even more weakly toothed *Lampetra aepyptera*, Ted M. Cavender and I have obtained with alizarin, staining results that parallel those of Zanandrea for *zanandreai*. Staining revealed embedded posterior teeth in some but not all specimens. Occasionally teeth may be found without staining. Vladykov and Kott (1976) placed *aepyptera* in their "genus" *Lampetra*, characterized by absence of posterior circumoral teeth. Since Vladykov et al. (1975) sometimes saw posterior circumorals (as Zanandrea had in *zanandreai*) and these did not fit their concept of *Lampetra aepyptera*, such specimens were placed in a "new species," *Lethenteron meridionale*.

Vladykov and Kott emphasize a statement by Zanandrea (1961: 526) quoted by Vladykov (1973: 208) and again by Vladykov and Kott (1982). Although quoted correctly, the statement "all brook lampreys caught in the waters of the north Italian plain have the characters on which Vladykov founded the species *L. zanandreai*, i.e. number and disposition of teeth on oral disc, numbers of trunk myomeres, coloration of ammocoetes, and body proportions. . ." is removed from the context of a paragraph that contends that *zanandreai* and *planeri* are valid, distinct, allopatric species. It is possible that unfortunate phraseology resulted from translation since the bulk of Zanandrea's other publications are in his native Italian. Be that as it may, it is inconceivable that in a summary paper published three years after his meticulous variational study of *zanandreai*, Zanandrea should retract his own data, as suggested by Vladykov and Kott. Vladykov (1973) himself quoted Zanandrea as reiterating in 1962 that he saw posterials in fresh specimens. Horny teeth probably do not dissolve in preservation but they may become buried in the soft disk tissues, and specialized techniques may be required to reveal them. Commenting on Zanandrea's (1958) observations, Vladykov and Follett (1965: 145) wrote "To reach a definite conclusion on the nature of such 'mandibular labials,' further study is required." No such further study has been attempted, but until and unless Zanandrea's data are disproved, I think they merit nothing but approbation.

In further support of his firm conviction that *zanandreai* always lacks posterior circumorals, Vladykov (1973: 209) noted that Zanandrea never removed that species from *Lampetra*. But Vladykov confused his own *Lampetra* [s.s.] with Zanandrea's *Lampetra* which [though narrower than *Lampetra* (s.l.) of Bailey 1980] included *japonica* (Zanandrea 1961: 531), assigned by Vladykov and Kott to *Lethenteron*.

As a final comment, I call attention to Zanandrea's observation of close morphological similarities between *zanandreai* and *aepyptera* (1958: 220, 223; 1961: 528), a point noted also by Potter (1980: 1606). The possibility of relationship of these two forms deserves further examination.

Newly described species

Vladykov and Kott appear to be annoyed by my use of the term "nominal species" for a number of lampreys recently described. My usage is customary, an unprejudiced expression that refers to valid species, synonyms, and/or species inquirendae, that is, named species. It was not a primary purpose of my comments (1980) to revise or evaluate the species of lampreys, so there was no reason to rework the ground plowed by Vladykov and Kott, among others. Their publications provide a wealth of data for study, but it seems to me presumptive to expect that other authors would necessarily accept all of their conclusions. I note above my basis for not accepting *Lethenteron meridionale*. In their recent list of California fishes, Hubbs et al. (1979) expressed reservations by a footnote to *Lampetra folletti*, *L. hubbsi*, and *L. pacifica* as follows: "The validity of localized forms is in need of critical appraisal." Robins et al. (1980) admitted two of these species (*hubbsi* and *pacifica*) in their names list of North American fishes, but withheld recognition of *folletti*, *alaskensis*, and *similis*. McPhail and Lindsey (1970) wrote of their comparison of 40 Michigan and Ontario *L. lamottei* [=*L. appendix*] and 43 Alaskan and Mackenzie *L. japonica* [including both parasitic *japonica* and nonparasitic (or satellite) *alaskensis*, not then described]: "The ranges and mean numbers of velar tentacles and of teeth on the infraoral tooth bar are virtually identical in the two forms. Muscle groove counts are lower in eastern *L. lamottei* (64−76, mean 67.4) than in Mackenzie (68−74, mean 71.7, seven specimens) or Alaskan (65−80, mean 69.4, 36 specimens) *L. japonica*. Further study may suggest that the two do not warrant specific separation. Presence or absence of a parasitic phase is not indication of specific differentiation, ..." Clearly, answers to some problems of lamprey systematics are unresolved.

As both parasitic and derived satellite species are commonly members of the same group taxon, it is unclear to me what

role greater variation in dentition of satellite than in parasitic species, or its genesis, plays in the development of a classification.

Status of Okkelbergia

The generic or subgeneric name *Okkelbergia* applies solely to the least brook lamprey *Lampetra aepyptera* (Abbott) from eastern United States. My visualization of *L. aepyptera*, since it includes *Lethenteron meridionale* Vladykov, Kott, and Pharand-Coad as a synonym (p. 1218), is very different from that of Vladykov and Kott.

Lampetra as constituted by Vladykov and Kott is an assemblage of forms in which posterior circumoral teeth have been lost or are in the process of reduction. In the phyletic line that includes the parasitic species *fluviatilis* and *ayresi* and the derived satellite species *planeri*, *richardsoni*, and *pacifica*, the loss of the posterior circumorals has been complete, but moderate or strong dentition is retained elsewhere, especially in the parasitic species. In contrast, in a second evolutionary line leading to *aepyptera*, the entire dentition is greatly reduced (Hubbs and Potter 1971: 39, 48–49, fig. 9), but in a pattern such that weak posterior circumorals may persist (Vladykov et al. 1975: fig. 3 and 6 [note that despite the disclaimer in the caption, fig. 6 of *aepyptera* shows at least three posterior circumorals on the left, one on the right]). A probable third convergent line leads to *zanandreai*. In it the dentition is moderately reduced, as in most nonparasitic species, and a weak posterior circumoral ring, or remnants thereof, may persist. As suggested by Hubbs and Potter (1971: 53), this seems to represent the *Lethenteron* line.

Given their belief "that inclusion of several groups with heterogeneous characters in the same genus hides individual peculiarities of each of the smaller groups" (Vladykov and Kott 1982), it is surprising that they include in *Lampetra* (s.s.) such a diversity of dentitional patterns, thus destroying its phyletic integrity. The frequent presence of posterior circumoral teeth is sufficient reason for exclusion of *aepyptera* from *Lampetra* (s.s.).

The true relationships of *Okkelbergia* remain uncertain, as shown by Hubbs and Potter (1971: 39, 48–49). As these authors suggested, a provisional placement, for which purpose I retained the name *Okkelbergia* as a subgenus, is still deemed appropriate. *Lampetra aepyptera* and *L. zanandreai* are the only brook lampreys for which stem (ancestral) species or group (subgenus) is not relatively certain; likely one or perhaps both are remote relatives of *L. japonica* or a related form, though some species of *Eudontomyzon* is not excluded as an ancestor.

Splitting vs. lumping

This issue, of course, is a matter of personal choice, and my position (1980) has already been expressed. With reference to interrelationships, the *Okkelbergia* problem (see above) documents the preference for subgenera. My view of this particular matter is based on the conclusion that *Lampetra* as defined by Vladykov and Kott is not a monophyletic group. They compare my *Lampetra* [=sensu lato] with their *Lampetra* [=sensu stricto], thus the rationale of their argument on genera vs. subgenera and zoogeography eludes me.

Name of the American brook lamprey

The manuscript by Bailey and Rohde on the name of the American brook lamprey (Bailey 1980) is still unpublished. In it we contend that the name *Petromyzon lamottenii* Lesueur [commonly emended to *lamottei*] is unidentifiable. Vladykov and Kott (1980) followed usage of the recent past in adopting this name for the American brook lamprey, but now (1982) identify the description with *Lampetra aepyptera* (Abbott). To avoid the inevitable nomenclatural confusion of transfer in name, however, they too, in effect, recommend suppression of Lesueur's name and continued use of *Lampetra aepyptera* for the least brook lamprey. Vladykov and Kott (1982) and Bailey and Rohde agree, also, that *Lampetra wilderi* Gage (1896) applies to the American brook lamprey, but we differ in our identification of the older name *Petromyzon appendix* DeKay (1842). Prior to 1922, authors applied both names (*appendix* and *wilderi*), but then Creaser and Hubbs (1922) synonymized them: "*Petromyzon appendix* DeKay we regard as assuredly based on the species currently known as *Lampetra* or *Entosphenus wilderi*."

By modern standards the description and illustration of *Petromyzon appendix* by DeKay leave much to be desired. Nevertheless, there are elements of the description that clearly dictate identification with the American brook lamprey, the only lamprey except *Petromyzon marinus* found in the area of Providence and the lower Hudson River, New York (Rohde 1980: 23), from which *appendix* was described. *Lampetra aepyptera* lives no closer than extreme southeastern Pennsylvania (Chesapeake Bay drainage) and southwestern Pennsylvania (Ohio River drainage), (Rohde and Jenkins 1980: 21). I examined the genital papilla in a sample of five Michigan specimens; it varies from 20.7 to 29.4 ($\bar{x}$ = 23.5) percent of branchial length, substantially longer than those measured by Vladykov and Kott. The length probably varies with breeding condition. These specimens compare very well in genital papilla length and other features with DeKay's figure of *Petromyzon appendix*. (The number of myomeres shown, about 60, is probably an artist's approximation; DeKay's figure of *Ammocoetes unicolor* [=*Ichthyomyzon* sp.] shows about 90 myomeres, far above the actual count in that genus.) I conclude that the American brook lamprey should be called *Lampetra appendix* (DeKay).

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My understanding of lamprey systematics has benefitted through conversations with Carl E. Bond. Marian K. Bailey, William A. Gosline, and Gerald R. Smith have read the manuscript and offered constructive suggestions — REEVE M. BAILEY, *Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109, USA*

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Comment on "Simple Growth Model for Salmonids in Hatcheries"

The following comment concerns the variations in the predictive accuracy of the "Simple growth model for salmonids in hatcheries" (*Can. J. Fish. Aquat. Sci.* 38: 649–656) and four errata in that paper.

Robert Huntley, a graduate student of Agricultural Economics at the University of Guelph, recently brought to my attention the fact that large variations can occur in the predicted final weights of fish by the use of different estimations (x) of 1/3, the weight exponent in the growth model $W_t^{1/3} = W_0^{1/3} + G_s t$ (W = weight in grams, G_s = T°C/1000, t = days).

I subsequently calculated final weights by the model using several estimations ($x = 0.3, 0.33, 0.333$, and 0.3333) of 1/3 for 5°C–15°C, $t = 365$, and $W_0 = 1$ g. Differences[1] between W_t^x and $W_t^{1/3}$ were then computed.

The final weight at the end of a time period can be predicted by a single calculation. In such a case, t would equal the number of days in the time period and the number of iterations (i) of the model would be 1. The final weight can also be predicted for the same time period by reducing t and increasing i. Some examples for one year are $t = 28$, $i = 13$; $t = 7$, $i = 52$; $t = 1$, $i = 365$. Because discrepancies[1] would be compounded by increasing i, the calculations above were repeated for these combinations of t and i.

The results of these calculations are presented in Table 1. Anyone contemplating the use of this model should be aware of these expected discrepancies. The use of 1/3 is recommended for the weight exponent. Otherwise, at least four 3's should be used after the decimal if i exceeds 1 — GEORGE K. IWAMA, *Fish Culture Extension Biologist, Ministry of Natural Resources, Fisheries Branch, Queen's Park, Toronto, Ont. M7A 1W3.*

[1]"Difference" and "discrepancy" are used synonomously in this context.

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ERRATA

1) Page 649 French abstract, line 3: first $W_0^{0.33}$ should be $W_t^{0.33}$.

2) Page 656, problem 2, second formula, denominator: t should be Gs.

3) Page 656, problem 3, first formula, numerator: 1.91 should be 1.71.

4) While 1/3 was used as the weight exponent in the development of the model, various decimal fractions were used in the paper. All decimal fractions should be replaced by 1/3.

TABLE 1. Percent discrepancies between W_t and $W_t^{1/3}$ resulting from using various estimations (x) of the weight exponent 1/3 in the growth model $W_t^{1/3} = W_0^{1/3} + Gst$ for a 1-yr period using four combinations of time (t in days) and the corresponding iterations (i) required for this period. T = temperature, °C.

	$x = 0.3$				$x = 0.33$				$x = 0.333$				$x = 0.3333$			
T	1i t=365	13i t=28	52i t=7	365i t=1	1i t=365	13i t=28	52i t=7	365i t=1	1i t=365	13i t=28	52i t=7	365i t=1	1i t=365	13i t=28	52i t=7	365i t=1
5	0	68.79	89.97	94.90	0	14.76	45,16	87,32	0	1.65	6.69	36.23	0	0.18	0.71	4.92
6	0	72.30	92.10	96.33	0	16.20	48.57	89.77	0	1.83	7.43	39.25	0	0.19	0.77	5.42
7	0	75.08	93.57	97.28	0	17.49	51.41	91.52	0	2.06	8.06	41.82	0	0.20	0.85	5.88
8	0	77.30	94.66	97.92	0	18.62	53.85	92.65	0	2.12	8.64	44.02	0	0.22	0.95	6.29
9	0	79.13	95.47	98.37	0	19.63	55.92	93.78	0	2.24	9.13	45.95	0	0.22	0.96	6.67
10	0	80.65	96.09	98.69	0	20.57	57.75	94.56	0	2.36	9.61	47.65	0	0.24	1.02	7.01
11	0	81.96	96.58	98.93	0	21.41	59.36	95.17	0	2.47	10.03	49.19	0	0.25	1.07	7.33
12	0	83.05	96.97	99.11	0	22.15	60.80	95.68	0	2.52	10.43	50.57	0	0.26	1.11	7.63
13	0	84.03	97.29	99.26	0	22.92	62.10	96.10	0	2.67	10.81	51.82	0	0.27	1.16	7.90
14	0	84.89	97.56	99.36	0	23.59	63.28	96.45	0	2.76	11.15	52.97	0	0.28	1.19	8.16
15	0	85.64	97.78	99.45	0	24.23	64.35	96.74	0	2.85	11.57	54.02	0	0.29	1.24	8.41

Trends in Fish Utilization. *J. J. Connell and R. Hardy. Published for the Buckland Foundation by Fishing News Books Ltd., Farnham, Surrey, England. 1982. 116 p. 6£ + 60p. post/packing.*

The authors of *Trends in Fish Utilization* draw on their long association with the Torry Research Station for much of the information presented in this book. Scientists at this laboratory, in common with other researchers throughout the world, have worked to determine methods of increasing the quantity and quality of fish protein resources and show ways in which previously unused or little used fish resources can be made available and acceptable as human foods. Much of what has been learned is embodied in this book.

Although it focuses on the general and more specific problems and means of alleviation associated with the more effective use of conventional fish resources accessible to the United Kingdom, it also examines with realism the potential use of less conventional or under or non-exploited fish and shellfish protein resources available or potentially available. The scope of this examination includes discussions of the various options for better or more complete use of resources which are near at hand, to more distant less readily available and less familiar resources.

Many of the concerns and ideas presented will be recognized by those who have an association with the multi and complex aspects of increasing and improving fish protein resource utilization.

Following an introductory chapter which discusses the rationale for the various hypotheses put forward, the authors present a systematic evaluation of the unused or underused species in order of their probability of potential for increased utilization. This evaluation considers the most likely determining factors contributing to their utility including ease of processing and handling and the practical processing options, potential consumer acceptance and an examination of how, where and when appropriate exploitation could be undertaken as well as current utilization figures and estimates of potential increases.

An important area of development, if costs can be rationalized, lies in can processing. Further diversification and upgrading in the quality of United Kingdom canned fish could increase home consumption leading to less dependence on imported products and open up the possibility of increased exports.

Also of topical importance is a section dealing with the emerging technology of mechanical flesh separation. The increasing focus of interest in this technology, if applied imaginatively, may do much to bring new resources to the consumer as well as improve the utilization efficiency of conventional resources and reduce the wastage associated with traditional practices.

Finally, *Trends in Fish Utilization* examines the constraints and opportunities contingent to improved marketing of the current and potential U.K. catch in the form of conventional and new and improved fishery products elucidating the need for an increased effort to understand consumer attitudes. The body of this book clearly shows the abundance of accessible technology available to increase and improve the efficiency of fish utilization, given the willingness of industry to adopt practical innovations to traditional methods. However, the authors recognize that the realization of accessing such technology will also depend largely on not only a greater insight or recognition of consumer needs but also in some serious effort to influence those needs through education and skillful and extensive market promotion.

In summary, this timely and useful reference will have wide application and interest to those concerned with the imaginative use of fish protein resources as a human food.

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(R410)

Marine Fish Larvae: morphology, ecology and relation to fisheries. *Edited by Reuben Lasker. Publisher, Washington Sea Grant Program. Distributor, University of Washington Press, Seattle. 1981. 131 p. $8.50 (U.S.).*

This book completes the two-part account of the early life history of marine fish based on a series of lectures presented at the College of Fisheries, University of Washington. Following part one on the egg stage by Hempel (1979), this volume comprises four chapters: Fisheries on Coastal Pelagic Schooling Fish by P. E. Smith, Feeding Ecology and Predation of Marine Fish Larvae by J. R. Hunter, The Role of a Stable Ocean in Larval Fish Survival and Subsequent Recruitment by R. Lasker, and Morphological and Functional Aspects of Marine Fish Larvae by H. G. Moser.

As one might guess from the list of authors, the book is based firmly on the fine research carried out by the fisheries ecology group at the Southwest Fisheries Center in La Jolla, California. Although close-to-home examples predominate, all topics are generally well related to world-wide research, and general principals are stressed.

The book is not particularly well organized and an introduction would have tied the lectures together. The first section of Smith's lecture, in which he describes the origins of the CalCOFI group in response to the sardine fishery collapse, could have formed a good basis for this. The remainder of his useful paper then could have been retitled "Sampling Strategies and Statistical Procedures" as this better describes his main theme; the title as it now stands being somewhat misleading.

Insofar as this book is mainly concerned with the problem of identifying and analyzing the causes of recruitment variability, the chapter on larval morphology appears out of place. A more coherent whole could have been achieved with the

inclusion of a section on larval physiology. With the exception of a subsection in Hunter's paper dealing with the nutritive value of prey, the subject is untouched here.

In past years Reuben Lasker's work, sometimes controversial but always imaginative and stimulating, has enriched the literature of larval fish ecology. Thus it was with a sense of disappointment I read his brief contribution to this volume. He outlines his hypothesis well, that wind events can cause mass mortality of first-feeding anchovy larvae, leading to pronounced reduction in year-class strength, but he fails to provide supporting data. The lack of supportive figures and tables is unfortunate, as they are available (Lasker 1981). He bases his ideas on Hjort's (1914) well-known critical period hypothesis, which remains controversial and not as widely attractive as he implies. As this is a review book, for the sake of balance, I would like to have seen some mention of the opposing view, for which there is good evidence, that mortality is cumulative and relatively continuous through egg and larval developmental stages.

Hunter's presentation is well documented and well organized into subsections with subtitles which are especially handy in a reference book. He is aware of the dangers of extrapolating laboratory studies to natural habitats and is careful to maintain the distinction between field and laboratory measurements. His review indicates gaps in our present knowledge and points out areas of profitable research.

I was not aware of the wide variety of fascinating morphological adaptations of larval fish and found Moser's descriptions enjoyable reading. The illustrations are good and the species depicted are identified with length and reference included. One annoyance is that many of the figure captions are merely species lists and the particular adaptation being illustrated is not stated.

In general the book is clear and concise with a good, diverse collection of references. I recommend it both to students as an introduction to larval fish ecology, and as a valuable reference for research scientists.

HEMPEL, G. 1979. Early life history of marine fish: the egg stage. Washington Sea Grant Publication; Univ. Washington Press, Seattle, WA.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 20: 1–228.

LASKER, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis mordax*) in the California current: contrasting years, 1975 through 1978. *In* R. Lasker and K. Sherman [ed.] The early life history of fish: recent studies. Rapp. R.-V. Reun. Cons. Perm. Int. Explor. Mer 178: 375–388.

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(R409)

Books Received/Livres reçus[1]

April/avril 1982

Aquacultural Engineering: an international journal. *Applied Science Publishers Ltd. (a company within Elsevier Science Publishers), London. 1982. Volume 1 (No. 1) 79 p. Four issues per volume; £47 per volume for U.K., USA, and Canada, £50 for other countries. Prices include postage and packing.* This new journal is dedicated to the dissemination of all aspects of the applied sciences necessary for the successful solution of the challenging practical engineering problems in aquaculture. Emphasis is on fundamental research and engineering methods. [R423]

Aquaculture and fish. *Commonwealth Agricultural Bureaux (CAB), Farnham Royal, Slough SL2 3BN, U.K. 1981. Compiled by Gillian Smith. 96 p. + 8 p. author index. £12.10 + carriage charge (USA & Canada 10% extra).* An annotated bibliography (No. F21) covers the literature abstracted for the 1980 volumes of CAB journals. [R424]

Biology of Freshwater Pollution. *C. F. Mason. Longman Group Limited, London and New York. 1981. 250 p. £5.50.* This work provides an introduction to the biological effects of water pollution and to ways of detecting, describing, and quantifying these effects in the field and in the laboratory. It presents a general overview. [R425]

Maryland's Oysters: research and management. *Victor S. Kennedy and Linda L. Breisch. A Maryland Sea Grant Publication, University of Maryland, College Park. 1982. 286 p. $8 (U.S.).* A critical review of the eastern oyster *Crassostrea virginica* and its Chesapeake Bay fishery. Included are sections entitled Biology of the Oyster, Maryland's Oyster Industry, and Questions for Further Research. [R426]

Maryland's Oysters: an annotated bibliography. *Victor S. Kennedy and Linda L. Breisch. A Maryland Sea Grant Publication, University of Maryland, College Park. 1981. 53 p. $3 (U.S.).* The 188 articles selected for annotation include a broad range of issues relevant to the Chesapeake Bay oyster fishery. This book and the one above are companions to "A Selected Bibliography of Worldwide Oyster Literature" by the same authors and published in 1980. [R427]

Stability and Trim of Fishing Vessels. *J. Anthony Hind. Fishing News Books Ltd., Farnham, Surrey, England. Second Edition 1982. 132 p. £7.50 + 75 p. post/packing.* The loading of vessels to secure maximum security and seakindliness is of vital importance to all fishermen and seamen. This book was written for those who need to pass examinations. There is, however, much for the practical man as well. [R428]

Hearing and Sound Communication in Fishes. *Edited by William N. Tavolga, Arthur N. Popper, and Richard R. Fay. Springer-Verlag, New York. 1981. 608 p. $49.80.* Papers originally presented at a meeting in April 1980 at Mote Marine Laboratory, Sarasota, Florida. Assesses the current state of knowledge of marine bio-acoustics and fish audition and predicts direction for further research. [R429]

The Early Life History of Fish: recent studies. The Second ICES Symposium, Woods Hole, April 2–5, 1979. *Co-edited by R. Lasker and K. Sherman. Rapports et Procès-Verbaux des Réunions. Volume 178. Available from Conseil International pour l'Exploration de la Mer, Palaegade 2-4, DK-1261, Copenhagen K. Denmark. 1981. 607 p. 350 Danish Kroner (about $45.36 U.S.) plus postage.* Includes significant advances in the study of early life history of fish, many of which are applicable to applied problems of population dynamics. This publication was reproduced by the staff of the Northwest Atlantic Fisheries Organization (NAFO). [R430]

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[1]Persons interested in reviewing books in this list should contact the Book Review Editor, Canadian Journal of Fisheries and Aquatic Sciences, Scientific Information and Publications Branch, Department of Fisheries and Oceans, Ottawa, Canada K1A 0E6.

[1]Les personnes intéressées à examiner les livres énumérés dans cette liste sont priées de communiquer avec le Rédacteur des comptes rendus, Journal canadien des sciences halieutiques et aquatiques, Direction de l'information et des publications scientifiques, Ottawa, Canada K1A 0E6.

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 37, No. 12 — paper by T. A. Jackson and R. E. Hecky: *Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone.*

PAGE 2308: Left column, line 2, "Metals bound in this summer" should read "Metals bound in this manner."

PAGE 2313: Figure 8D, lettering for the scale on the horizontal axis of the graph, "Thousands of μmol org. C/g" should read "μmol org. C/g."

VOLUME 38, No. 9 — paper by T. F. Nalepa and A. Robertson: *Screen mesh size affects estimates of macro- and meio-benthos abundance and biomass in the Great Lakes.*

PAGE 1027: Key words, "meibenthos" should read "meiobenthos." Right column, last line, "benthis" should read "benthic."

PAGE 1031: Left column, subheading, "Variations in macrobenthos retention in relation to sampling depth and data" should read "Variations in macrobenthos retention in relation to sampling depth and date."

PAGE 1032: Table 4, box heading 1977, column Nov. 17, line 9 below box heading rule, "2.57" should read "25.7."

VOLUME 38, No. 12 — paper by N. Ryman and G. Ståhl: *Genetic perspectives of the identification and conservation of Scandinavian stocks of fish.*

PAGE 1572: This figure has incorrect scales for both genetic identity and time since divergence and is replaced by:

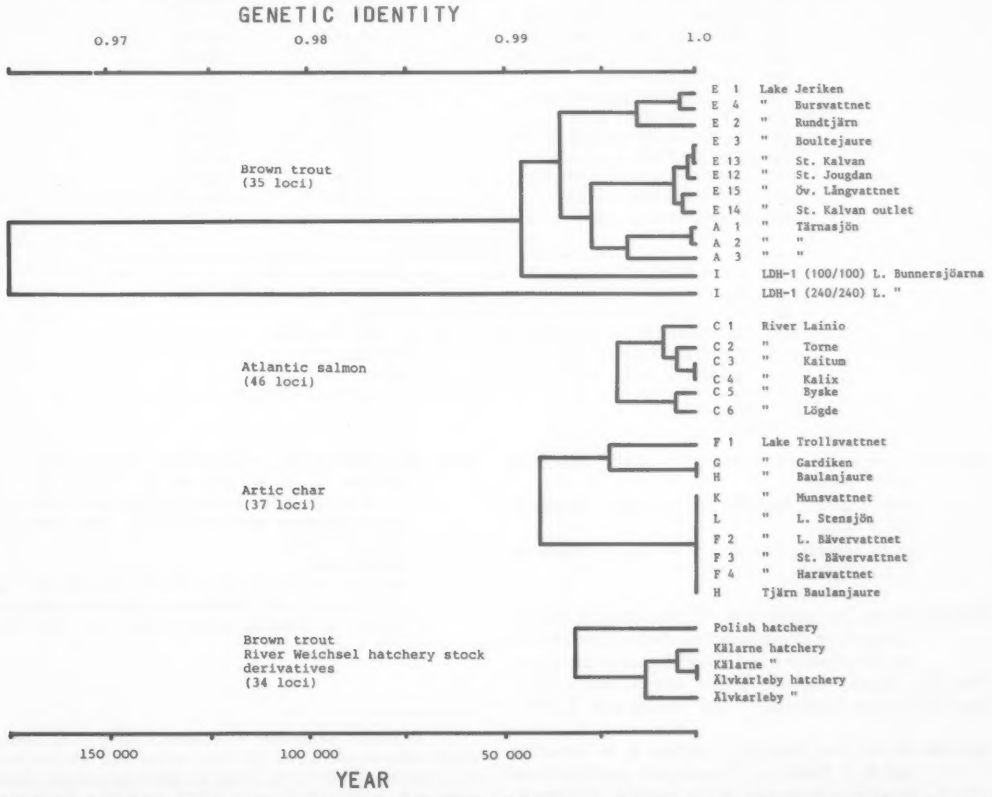

FIG. 3. Dendrograms (UPGMA, Sneath and Sokal 1973) summarizing the genetic relationships among populations of the three species investigated. (The dendrograms were constructed from gene identity (*I*) values (Nei 1975) based on the allele frequencies given in Tables 1–3.) Effective divergence time was estimated according to Nei (1975, p. 193).

VOLUME 38, No. 12 — paper by P. J. Colby and S. J. Nepszy: *Variation among stocks of walleye (Stizostedion vitreum vitreum): management implications.*

PAGE 1821: line 4 of Fig. 5 caption, "$pj\sqrt{rx}$" should read "$\frac{pj}{\sqrt{rx}}$."

VOLUME 39, No. 1 — The collection of papers "Fish Reproduction: Behavior and Endocrinology" was edited by Special Editor Dr Edward M. Donaldson. Our apologies to Dr Donaldson for the omission of his title and recognition of his special efforts toward publication of the papers.

VOLUME 39, No. 1 — paper by H.-R. Lin: *Polycultural system of freshwater fish in China.*

PAGE 143: Left column, 2nd paragraph, line 1 of text, "temperature" should read "temperate."

PAGE 144: Right column, 5th paragraph, line 2, "round head bream and similar to" should read "round head bream are similar to."

PAGE 148: Right column, 1st paragraph, line 1, "The main problem is brooder pond management" should read "The main problem in brooder pond management."

VOLUME 39, No. 2 — paper by J. M. Hanson and W. C. Leggett: *Empirical prediction of fish biomass and yield.**

PAGE 259: Table 2 should read

TABLE 2. Regression equations, based on data set 2, for estimating the fish yield (FY in kg/ha) from mean depth ($\bar{z}$ in m), lake surface area (A_0 in km^2), total dissolved solids (TDS in mg/L), and total phosphorus concentration (TP in μg/L). MEI = TDS/$\bar{z}$.

	Simple regressions	r^2	P[a]
(1)	FY=0.072 TP+0.792	0.84	<0.001
(2)	log FY=1.021 log TP−1.148	0.87	<0.001
(3)	FY=0.092 TDS−0.499	0.43	<0.001
(4)	log FY=0.944 log TDS−1.204	0.33	<0.010
(5)	FY=0.176 $\bar{z}$+4.412	0.14	<0.097
(6)	log FY=0.665 log $\bar{z}$−0.146	0.10	<0.159
(7)	FY=0.160 MEI+4.761	0.05	<0.350
(8)	log FY=0.191 log MEI+0.260	0.02	<0.500
(9)	FY=−0.00006 A_0+6.670	0.00	<0.990
(10)	log FY=0.004 log A_0+0.280	0.00	<0.930
(11)	TP=0.976 TDS + 4.568	0.30	<0.010
	Multiple regressions		
(12)	FY=0.069 TP+0.156 $\bar{z}$+0.007 TDS−1.297	R^2=0.97	P[b]<0.001
(13)	log FY=0.973 log TP+0.391 log $\bar{z}$−0.016 TDS−1.377	R^2=0.92	P[b]<0.001
(14)	FY=0.071 TP+0.165 $\bar{z}$−1.164	R^2=0.96	P[b]<0.001
(15)	log FY=0.967 log TP+0.384 log $\bar{z}$−1.390	R^2=0.92	P[b]<0.001
(16)	FY=0.084 TDS+0.068 $\bar{z}$−0.679	R^2=0.44	P[b]<0.005
(17)	log FY=0.789 log TDS+0.349 log $\bar{z}$−1.231	R^2=0.37	P[b]<0.015

[a] t-test.
[b] F-test.

PAGE 259: Left column, line 18, "(r^2 = 0.62)" should be "(r^2 = 0.43)."
Left column, line 20, "(r^2 = 0.40)" should be "(r^2 = 0.30)."
Right column, line 4, "(r^2 = 0.62)" should be "(r^2 = 0.44)."

VOLUME 39, No. 2 — paper by R. W. Nero and I. J. Davies: *Comparison of two sampling methods for estimating the abundance and distribution of Mysis relicta.*

PAGE 352: Figure 1 caption, "L.239" should read "L.223."

PAGE 353: Figure 2 caption, "L.223" should read "L.239."

VOLUME 39, No. 4 — paper by D. Mathur, R. M. Schutsky, and E. J. Purdy Jr.: *Temperature preference and avoidance responses of the crayfish, Orconectes obscurus, and associated statistical problems.*

PAGE 553: Right column, 4th reference, lines 14−16,

MATHUR, D., R. M. SCHUTSKY, E. J. PURDY JR., AND C. A. SILVER. 1981. Analysis of geographic variations in acute temperature preference of fishes. Trans. Am. Fish. Soc. 110: 1−13.

should read

MATHUR, D., R. M. SCHUTSKY, E. J. PURDY JR., AND C. A. SILVER. 1981. Similarities in acute temperature preferences of freshwater fishes. Trans. Am. Fish. Soc. 110: 1−13.

*Dr E. Prepas (Department of Zoology, University of Alberta) kindly noted an error in two TDS values in data set 2. We have rerun our analyses and find that the results strengthen our previous conclusions on the relative effectiveness of TDS and MEI as predictors of fish yield.

VOLUME 39, No. 4 — paper by R. C. Cook: *Stock identification of sockeye salmon (Oncorhynchus nerka) with scale pattern recognition.*

PAGE 614: Left column, the equation

$$g(\hat{\sigma}_a) = \max \sum_{j=1}^{n_a} f_a^j(\mathbf{X}_{aj}),\ \hat{\sigma} > 0$$

should read

$$g(\hat{\sigma}_a) = \max \prod_{j=1}^{n_a} f_a^j(\mathbf{X}_{aj}),\ \hat{\sigma} > 0$$

VOLUME 39, No. 5 — paper by R. J. Beamish: ***Lampetra macrostoma**, a new species of freshwater parasitic lamprey from the west coast of Canada.*

PAGE 747: Left colum, 2nd and 3rd references should read

BEAMISH, R. J. 1980. The adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

BEAMISH, R. J., AND E. J. CROSSMAN. 1977. Validity of the subspecies designation for the dwarf white sucker (*Catostomus commersoni utawana*). J. Fish. Res. Board Can. 34: 371–378.

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Maximum tolerable level, digestion, and metabolism of D-glucose (cerelose) in rainbow trout (*Salmo gairdneri*) reared on a practical trout diet
J. W. Hilton, J. L. Atkinson, and S. J. Slinger

Ecological responses of hydropsychid caddisflies to stream regulation
F. R. Hauer and J. A. Stanford

Effect of growth rate and size of fish on rate of intoxication by waterborne lead
P. V. Hodson, D. G. Dixon, D. J. Spry, D. M. Whittle, and J. B. Sprague

Discount factors and risk aversion in managing random fish populations **R. Mendelssohn**

Analysis of longitudinal zonation and the river continuum concept in the Oldman–South Saskatchewan River system **J. M. Culp and R. W. Davies**

Population characteristics of juvenile coho salmon (*Oncorhynchus kisutch*) overwintering in riverine ponds **N. P. Peterson**

A method for predicting winter oxygen profiles in ice-covered Ontario lakes
M. B. Jackson and D. C. Lasenby

Ability of standard toxicity tests to predict the effects of the insecticide diflubenzuron on laboratory stream communities **S. R. Hansen and R. R. Garton**

Influence of hook size in the Hawaiian deep-sea handline fishery **S. Ralston**

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Immigration of juvenile coho salmon (*Oncorhynchus kisutch*) into riverine ponds
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Capacity reduction on Norwegian industrial fisheries **S. D. Flåm and S. Storøy**

Blood protozoa as an aid for separating stocks of Greenland halibut, *Reinhardtius hippoglossoides*, in the northwestern Atlantic
R. A. Khan, M. Dawe, R. Bowering, and R. K. Misra

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